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UNIVERSITY OF ALBERTA

PATTERNS OF VARIATION IN THE BROWN MOSS MEESIA TRIQUETRA OVER AN ARCTIC-BOREAL GRADIENT

BY

R. JOAN S. MONTAGNES

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN

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MASTER OF SCIENCE

IN

PLANT ECOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

FALL, 1990

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Date: September 15, 1992

Abstract

A long-standing debate exists over the rate at which bryophytes are capable of evolving. Variation in Meesia triquetra (Richt.) Aongstr. over an arctic-boreal gradient was investigated to examine the evolutionary potential of this moss.

Meesia triquetra is a rich fen indicator species. Its current distribution in North America is documented from northern Ellesmere Island south to California in the west and Pennsylvania in the east, and from western Alaska east to Newfoundland. All quaternary subfossil records lie in the same geographic area as extant records except for one in Iowa and another in Ohio, both of which lie south of the current range.

Surface water of fens in which Meesia triquetra occurs generally has high pH (6.5 - 7.5) and high calcium concentrations (30 - 60 $mg \cdot l^{-1}$) and varies significantly only in phosphorus concentrations, turbidity, and pH along an arctic-boreal gradient. Some differences in water quality are evident among fens along the gradient, although these differences may be results of yearly climatic variation.

Overall morphology and individual morphological characters of Meesia triquetra vary significantly with latitude and the variation is substantial enough to allow discrimination among specimens from the Boreal Forest, Low Arctic, and High Arctic ecoclimatic regions by morphology alone. Multivariate analysis of variance indicates that significant morphological differences exist among specimens from the three ecoclimatic regions.

Annual growth increment length decreases with latitude. In a common garden experiment, under boreal conditions, stems from an arctic population grew less than stems from a boreal population, regardless of the aquatic environment in which they were grown, indicating that populations of Meesia triquetra have adapted to local environments.

The amount of electrophoretically detectable genetic diversity in Meesia triquetra decreases with latitude. Meesia triquetra has genetic variability values, both in terms of

diversity (0.151) and identity among populations (0.9 - 1.0), comparable to many vascular plants and animal species. The genetic diversity of samples of a population is proportional to the diversity in the whole population and the genetic distance between samples and home populations decreases with latitude.

Meesia triquetra demonstrates an active potential to evolve based on the variation it exhibits in morphology, growth rate, and genetics. I suggest that if M. triquetra evolves slowly, it is because it is well suited to its environment, not because it possesses a low potential for evolution.

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I. Introduction.

Throughout the last decade bryologists have debated the rate of evolution in mosses and liverworts. Traditional views regard bryophytes as plants low on the evolutionary scale in relation to ferns, gymnosperms, and angiosperms, as they are phylogenetically older than these plant groups but far less differentiated (Crum 1972; and Szweykowski 1984). Differentiation of the major taxonomic divisions within the bryophytes (mosses, liverworts, and hornworts) was completed by the Permian period (Anderson 1980; and Ennos 1990), and modern moss genera and species were present by the Cenozoic (Vitt 1984). Morphological similarities among congeners are used as evidence of slow evolution (e.g. Daniels 1982). In fact, Crum (1966) has gone as far as to say that evolution at the specific level appears to be at a standstill.

Five lines of evidence support the view that bryophytes have a low evolutionary rate. First, some taxonomic groups are morphologically uniform with very few varieties or endemics and a small number of species per genus, which, according to Crum (1972), indicates a depleted biotype and a genetic poverty associated with the old age of the phylum. Also, the fossil record indicates that bryophytes diversified into the major taxonomic divisions of mosses, liverworts, and hornworts by the Permian period and that very few major morphological changes have occurred since (Anderson 1963; Crum 1972; Cummins and Wyatt 1981; Dewey 1989; Krzakowa and Szweykowski 1979; and Wyatt et al. 1989). However, several bryologists have suggested that the fossil record is far too scant to be used as conclusive evidence in the debate on the rate of evolution in bryophytes (Kharma 1964; Krassilov and Schuster 1984; and Miller 1984).

Second, some species of bryophytes are found in disjunct populations as far apart as the two poles. Tracheophytes, with similar distributions, have undergone speciation so that they are related to each other at the generic or familial rank, while disjunct populations of bryophytes are often of the same species. Such disjuncts can be viewed as relict

populations, or as Crum (1972) wrote: "unmoving Sphinxes of the past", that have not undergone adaptive radiation or even random genetic drift to render disjunct populations taxonomically different from the rest of the species (Anderson 1963; Crum 1966; Cummins and Wyatt 1981; Dewey 1989; Krzakowa and Szweykowski 1979; and Szweykowski 1984). Furthermore, many bryophytes of disjunct populations have become non-sexual which decreases their chances for evolution (Longton 1976).

Third, many bryologists believe that the slow rate of evolution in mosses and liverworts is chiefly due to the dominant haplophase in the bryophyte life cycle. Diploids have the evolutionary advantages of increased genetic variation due to heterozygosity, the ability to aquire mutations twice as fast, and the ability to mask deleterious recessive alleles (Innes 1990). Haploid organisms, on the other hand, are believed to have low genetic diversity because a slightly deleterious mutation will be strongly selected against in the gametophyte stage, and since mutations that are deleterious in one environment may be advantageous in another, the chances of adapting to new environments through mutation alone are reduced (Crum 1972; Cummins and Wyatt 1981; Daniels 1982; Innes 1990; Krzakowa and Sweykowski 1979; Longton 1976; and Sweykowski 1984; Yamazaki 1981). It is difficult to test this theory in mosses because of the slow growth rate , however, Paquin and Adams (1983) found that diploid yeast evolved 1.6 times faster than haploid yeast. Although mutations are more often deleterious, an advantageous mutation in a haploid organism would be selected for strongly, and any mutation that was not selected against may reproduce rapidly in mosses through vegetative reproduction (Anderson 1963).

Fourth, because of their small stature and relatively restricted niche range, bryophyte species are thought to be subjected to very few new selective pressures (Crum 1966; Cummins and Wyatt 1981; Dewey 1989; and Longton 1976). Mosses can avoid macro-environmental change because they are well suited to specific micro-environments,

thus they avoid the pressures which are exerted on larger plants though geologic time (Anderson 1963; and Crum 1972) or presumeably over large environmental gradients such as changes in latitude. Supposedly because bryophytes are not subjected to new selective pressures, they do not undergo adaptation, hence they appear to have a low evolutionary potential.

Finally, bryophytes have a particularly short gene flow distance which is thought to increase inbreeding, reduce sexual recombination, and reduce the rate of evolution (Anderson 1980; and Cummins and Wyatt 1981). Sperm require a continuous film of water from antheridium to archegonium to achieve fertilization. This provides a formidable reproductive barrier to monoicous species and even more of a barrier to dioicous and phyllodioicous species which are, by definition, obligate outcrossers (Khanna 1964). Some moss species increase the distance sperm can travel by producing antheridia in splash cups, but even this mechanism increases gene flow only to a maximum of approximately 15 cm (Wyatt 1982). Potentially, spores can waft into the upper atmosphere and be carried for 19,200 kilometers or more (Longton 1976). Although long range dispersal may be hindered by the size of some spores (larger than 25 μm), spores may be transported long distances by animal vectors (van Zanten and Pocs 1981). According to several bryologists, there is a trend towards monoicy and even abandonment of sexual reproduction in mosses, presumably because of the costs associated with long distance sperm travel (Cummins and Wyatt 1981; Dewey 1989; and Khanna 1964), thus species can become almost genetically identical throughout their range (Anderson 1963).

Fragmentation can become an important mode of reproduction and gene dispersal as almost every part of the moss plant, except the antheridia, can regenerate (Anderson 1980). Fragmentation and vegetative reproduction are particularly important in polar regions where sporophyte production is much lower than in temperate or tropical regions (Crum 1972; Holman 1960; Longton 1976; Schofield 1985; and Smith 1987). Inbreeding

and vegetative reproduction lead to reduced gene diversity which in turn reduces the evolutionary flexibility of a species. Prior gene diversity is required before temporal, spatial, or ecological reproductive isolating mechanisms can affect evolutionary rates (Ennos 1990; Farris 1988; and MacNaire 1989), where gene diversity (H) is the probability of nonidentity of two randomly chosen genes from within a population (Nei 1973). Therefore, we can expect that genetic diversity will be reduced in arctic mosses relative to mosses of lower latitudes, and possibly that populations of mosses in the north will have lower genetic diversities relative to their conspecifics in the south. Genetic diversity levels may have ramifications for plant habitat preference, morphological variation, and variation in growth responses.

These five lines of evidence have led bryologists to believe that evolution is slow in the bryophytes. Crum (1972) went as far as to say that mosses are "evolutionary failures" and that "for ecological success they have paid in genetic uniformity and slow speciation", however, all of the above hypotheses are based on inference and not on empirical data. Variation is the fuel that drives all evolutionary processes (Stearns 1989), therefore we must investigate variation in actual bryophyte populations to determine whether or not bryophytes have the potential to evolve. Variation due to natural selection is most evident along environmental gradients. For this study I have chosen a long environmental gradient that combines changes in many ecological factors.

The latitudinal gradient

The environmental gradient from temperate to polar regions has long interested plant ecologists both for community study and autecology. The length of this gradient and its complexity give ample opportunity to study plant responses to environmental stimuli. Arctic adaptations in vascular plants have been well documented (Bliss 1962; Chapin 1983; Corbet 1969; Love and Love 1974; and Savile 1972). The arctic climate is

characterized by a short, cold growing season, strong winds, low light intensity, low precipitation, and the long arctic day coupled with the equally long arctic night. Low nutrient availability, caused by low decomposition rates and slow soil forming processes, is an indirect effect of the harsh climate. Low temperatures, low nutrient availability, low light intensity, and the short growing season are considered the major factors controlling plant growth in the arctic (Billings 1987; Bliss 1962; Chapin 1983; Savile 1972; Weilgolaski 1980; and Warren Wilson 1966). Severe arctic conditions, however, may pose more of an obstacle to vascular plants than bryophytes (Brassard 1974) as is shown by the dominance of mosses in many high latitude habitats and the fact that bryophyte production is much less reduced with increasing latitude than production in vascular plants (Weilgolaski 1980). Despite low temperatures, arctic environments experience fewer freeze/thaw cycles per year than boreal regions because of the long photoperiod, thus the climate is somewhat ameliorated (Corbet 1969). In addition, the arctic climate is more variable from year to year than boreal climates (Addison and Bliss 1980; Bliss 1962; Bliss et al. 1973; Savile 1972; and Warren Wilson 1966).

Ecology and patterns of variation

In addition to investigating the patterns of variation in Meesia triquetra (Richt.) Aongstr., this study also will describe the habitat of this moss and its distribution in North America and Greenland. It is important to understand the full biology of the study species before setting out on exploration of its behavior along a latitudinal gradient. Once the ecology and distribution of M. triquetra has been outlined in the first chapter, patterns of variation in the habitat, morphology, growth, and genetics of the moss will be investigated and the findings of these studies will be related to the debate on the rate of evolution in bryophytes.

1. Habitat.

Mire water chemistry has been extensvely studied in relation to mire floristics and classification. Bogs and fens lie on a gradient of increasing pH, alkalinity, and cation concentration from oligotrophic bog to minerotrophic extreme-rich fen (Schwintzer and Tomberlin 1982; Sjors 1961; Slack et al. 1980; and Vitt and Bayley 1984). Gorham and Pearshall (1956) stated that conductivities are usually above 70 µS in fens and below 70 µS in bogs and that nutrient levels are higher in fens than in bogs, however Swintzer and Tomberlin (1982) and Vitt and Chee (1990) have found that nutrient levels can be lower in fens than in bogs and the latter group have suggested that it is the water flow which regulates nutrient availability and not necessarily the concentration of nutrients in the water.

No specific bryophyte species distributions have been directly linked to environmental parameters (Brown 1982), but various studies have been made to determine indicator species and species assemblages associated with particular environments (Vitt and Slack 1984). For example, the bryophyte vegetation in streams of the Canadian Rocky Mountains was statistically separated into different associations on the basis of Ca and Mg concentrations as well as soil texture and water level (Vitt et al. 1986). The species composition of peatlands in the Netherlands have changed due to decreases in Ca in the surface water which indicates the sensitivity of peatland species to water chemistry (Wassen et al. 1989).

Water chemistry can have substantial effects on the morphology and growth of moss species. Rhynchostegium riparioides (Hedw.) C. Jens varies in size, leaf length, leaf shape, and denticulation along a gradient from calcareous head waters and springs to large rivers with high nutrient concentrations (Wehr and Whitton 1986). In the laboratory, Austin and Weider (1987) found that elevated levels of H, NO_3, NH_4, and SO_4 affected

the growth and chlorophyll content of three Sphagnum species, and that the response was species dependent. Ferguson et al. (1984) have suggested that the decline of Sphagnum bogs in the South Penines, U.K. and the failure of transplants there is due to elevated nitrogen and phosphorus levels in addition to elevated sulphur levels in precipitation.

In her 1982 work on bryophytes in relation to niche theory, Slack defined the realized niche as the ecological space in which a species can exist limited by physiological factors. Surface water chemistry is part of a complex set of environmental parameters which define the niches of mire species. For instance, Vitt and Slack (1984) found that pH, Ca, and Mg are important in niche separation in Sphagnum. Slack (1982) stated that the realized niche can change from locality to locality because of the changing demands on the physiology of the species in question. The habitat section of this study examines the variation in surface water chemistry of fens in which Meesia triquetra occurs along an arctic-boreal gradient, to determine whether the chemical aspect of the niche of this moss changes over a wide range of macroclimates.

2. Morphology

Morphological variation in plants, due to genotypic variation and phenotypic plasticity, can enable species distributions to expand, thereby exposing populations to new selective pressures (Longton 1979b; and Stearns 1989). Morphological variation may be used as an indicator of evolutionary potential in the long-standing debate on the rate of evolution in bryophytes.

Each morphological character in a plant is associated with a plasticity character which varies as a function of environmental signals; the relationship between environment and morphology may be called a reaction norm. The norm is genetically controlled and subject to natural selection (Bradshaw 1965; and Stearns 1989). Phenotypic plasticity may or may not be adaptive. Adaptive characters increase survival, reproduction, or growth.

A plant not physiologically buffered against environmental stresses will respond in a non-adaptive plastic fashion such as reduced production or fertility (Schlichting 1986).

Some bryophytes are well known to exhibit morphological variation (Longton 1979b; and Schofield 1981). Isothecium stoloniferum Brid. is nearly dendroid when growing on the bases of tree trunks, but is distinctly pinnate in humid open forests, and pendent when found on branches and trunks in humid closed forests (Schofield 1981). The Macrocoma tenue-M. sullivantii complex varies in leaf and cell length throughout its distribution in the Americas, Africa, Asia, and the South Pacific (Vitt 1981). Glime and Raeymaekers (1987) found that species of Fontinalis varied in branch production along a temperature gradient. Vitt and Horton (1976) found patterns of variation in leaf shape in North American Climacium americanum Brid. and C. dendroides (Hedw.) Web. et Mohr. which followed a northwest-southeast gradient from Alaska to Florida. Three Schlotheimia species varied along a latitudinal gradient from 10° to 60° S in Australia and New Zealand. Schlotheimia brownii Schwaegr. varied in cusp length, while S. knightii C. Meull and S. campbelliana C. Meull. varied in cell length parameters. Each of these three congeners exhibited different patterns of morphological variation (Vitt 1989).

Few comprehensive studies have been made on morphological variation in bryophytes along latitudinal gradients. Hylocomium splendens (Hedw.) B.S.G. exhibits striking morphological variation from temperate to arctic habitats. Subspecies giganteum Pers. ex Vitt, found along the west coast of Canada, grows in wefts and possesses the characteristic "stair-step" frond; whereas variety obtusifolia (Geh.) Par., found north of treeline, lacks this character. The variety splendens is intermediate to giganteum and obtusifolia in many characters.

Longton (1974) found that Polytrichum strictum Brid. decreased in its annual growth increment weight and length, the number of leaves per annual growth increment, and leaf length along latitudinal gradients from the tropics to the extreme polar locations of

Galindez Island (65° 15' S) and Rankin Inlet, N.W.T. (62° 45' N). He determined experimentally that these differences were controlled both endogenously and exogenously. Longton (1979a) suggested that P. strictum is widespread because of its ability to morphologically adapt to a variety of environments both genetically and through phenotypic plasticity. Vitt (1991), on the other hand, found no significant correlation between annual growth increment length and latitude in P. strictum along a gradient from 49° to 76° N. Longton's southern specimens were collected from Manitoba, while Vitt's southern specimens were collected from Alberta. It has been suggested that the discrepancey between these two studies exists because the mean summer temperature in Alberta is lower than that of Manitoba (Vitt pers. comm.).

Longton (1981) grew populations of Bryum argenteum Hedw. collected from polar, temperate, and tropical localities and found that morphological variation amongst the populations, in particular in the antarctic population in contrast with the others, decreased substantially in a common garden experiment. The morphological section of this study will determine the degree of morphological variation in Meesia triquetra over an arctic-boreal gradient and will relate that variation to the potential of M. triquetra to evolve.

3. Growth

Several authors have examined variation in bryophyte growth. Longton (1972 and 1979b) found that Polytrichum alpestre Hopp. decreased in annual growth increment length and weight, leaf length, and number of leaves produced per year with latitude. Sphagnum species have a higher production rate in shaded areas than in open areas at Barrow, Alaska (Murray et al. 1989). Wehr and Whitton (1986) found that Rhynchostegium riparioides varies in robustness, leaf shape, and length, and in degree of leaf denticulation from springs and calcareous head-waters to large rivers with high sodium, ammonium, and phosphate concentrations. Busby et al. (1978) found that growth in Hylocomium

spendens was controlled by overstory vegetation and that Tomethypnum nitens (Hedw.) Loesk growth was controlled by precipitation. Pohlia wahlenbergii (Web. et Mohr.) Andrews was found to be more productive along stream banks than on hill sides (Clarke et al. 1971). Finally, Hylocomnum splendens shows great morphological diversity from a gigantic west coast form to a tundra from which lacks the characteristic stair-step fronds (Vitt 1991).

Although many authors have examined variation in bryophytes, few have followed through in their studies with common garden experiments or reciprocal transplants to determine whether the variation is a result of genetic differentiation or phenotypic plasticity. Only these sorts of experiments can be used to interpret variation. For instance, in greenhouse experiments, Birse (1957) found that moss growth forms were environmentally induced, not genetically controlled. Longton (1974) found that populations of Polytrichum strictum taken from a range of environments along a latitudinal gradient lost morphological differences when grown in a common garden . Similar results were obtained with Bryum argenteum (Longton 1981). He also found the antarctic populations of Polytrichum alpestre could maintain a positive net carbon gain in temperatures too low for boreal populations, which indicates ecotypic differences between the two populations. Kallio and Saarnio (1986) preformed reciprocal transplant studies along a latitudinal gradient on Pleurozium shreberi (Brid.) Mitt. , Hylocomium splendens, and Racomitrium lanuginosum (Hedw.) Brid. and found that photosynthesis increased in the plants which were moved south. They also found that this change in photosynthesis was not in fact genetic differentiation between the arctic and boreal plants, but a plastic response to light levels; after two years the photosynthetic apparatus had changed and the photosynthetic rates decreased to normal ranges for boreal plants.

Vitt and Pakarinen (1977) were able to use the well developed annual growth increment markers in Meesia triquetra to estimate annual production of the bryophyte layer

in a hummocky sedge meadow at Truelove Lowland, Devon Island in the Canadian Arctic. This moss is subject to a variety of environmental conditions over its extensive range. The objective of the growth response section of this study was to determine whether the variation in growth rate among populations of M. triquetra along an arctic-boreal gradient is a result of a plastic response to an environmental gradient or a result of genetic variation due to natural selection.

4. Population genetics

Evolution is based on changes in gene frequencies and so it is at gene frequency that we should look for information on the rate of evolution in bryophytes (Krzakowa and Szweykowski 1979; and Wyatt 1982). Electrophoresis is a technique of extracting and analysing the electric mobility of soluble protiens to compare the amino acid composition of protiens to determine the degree of genetic differentiation between individual organisms (Hofman 1988; and Stebbins 1989). Isozymes and allozymes are expressed as bands on a gel medium. Isozymes (multiple molecular forms of enzymes) are enzymes that share a common substrate but differ in electric mobility, whereas allozymes are allelic products from a single molecular form of an isozyme which differ in electric mobility (Wendel and Weeden 1989).

Several electrophoretic studies indicate that the level of genetic diversity in bryophytes is much higher than expected and is in some species comparable to genetic diversity in angiosperms. For instance, the liverwort Conocephalum conicum (L.) Dum. has a genetic variability comparable to many diploid species of vascular plants. Seven of 11 enzyme systems examined in this liverwort were found to vary in their polymorphism at two different levels (Yamazaki 1981). At the world level, there are two isolated forms which were later discovered to have different morphology, growth rates, and produced different phenolic compounds. Over 1000 specimens were examined and no indication of

recombination between the two types was found (Sweykowski 1982). The second level of variation is at the local level where diversity was higher than at the world level because of many rare alleles (Sweykowski 1984).

Electrophoresis has been used in taxonomic investigations of the genus Pellia. Krzakowa (1981) found P. endiviifolia Dum. and P. epiphyllia (L.) Corda to be distinct species and that many other Pellia species were synonomous with one or the other taxon, while Zielinski (1987) found that populations of P. endiviifolia in Poland and Japan were as genetically different as many angiosperm species. Zielinski also found that P. neesiana (Gottsche) Limpr. and P. borealis had genetic diversities much lower than most angiosperm species (H_t = 0.025 and 0.045 respectively). Possibly the descrepancy in these studies resulted because Krzakowa used only peroxidase to indicate differences among species, whereas Zielinski used 10 different enzymes. Peroxidase and esterase are nonspecific enzymes which often produce many loci leaving these systems difficult to interpret; also the activity of these enzymes are known to be affected by environmental conditions (Wyatt et al. 1989). If peroxidase or esterase markers are used in determining genetic variability they should not be used alone but in conjunction with more reliable systems. Much of the work done on genetic diversity in bryophytes has utilized these questionable enzymes. In another example Krzakowa and Szweykowski (1979) used three peroxidase loci to examine variation in Plagiochilia asplenioides (L.) Dum.. They found substantial differences in the genetic structure between two races within Poland and a high level of variation within colonies occurring within populations. It is unfortunate that such good work must be regarded as suspect until it is supported by further investigations.

There are, however, many studies soundly based on several reliable enzyme systems. Szweykowski and Zielinski (1983) found four genotypes of Plagiothecium undulatum (Hedw.) B.S.G. in Poland, and that individual colonies of this moss were

electrophoretically monomorphic. Shaw et al. (1987) found genetic differences between Climacium americanum Brid. and C. kindbergii (Ren. et Card.) Grout and concluded that C. kindbergii was not a variety of C. americanum as has long been thought (Horton and Vitt 1976), but a separate species. Electrophoretic and morphological differences indicate a linkage disequilibrium between the two species. This conclusion is further supported by the fact that the species are often found growing together which indicates that they have become reproductively isolated. In fact, C. kindbergii plants from one site are more like C. kindbergii plants from another site, than like C. americanum plants at the same site. De Vries et al. (1989) found moderate to high levels of genetic diversity in populations of Racopilum species that were comparable to phanerogam populations. Dewey (1988) was able to confirm the distinction between Riccia dictyospora Howe and R. mcalisteri Howe with electrophoresis although genetic variability in the genus was quite low. He suggested that other species in the genus have been classified based on phenotypic differentiation rather than genetic divergence. Boisselier-Dubayle and Bischler (1989) found a good correlation between habitat and electrophoretic data in Marchantia polymorpha L. They found that plants growing in urban and naturally wet habitats differed genetically and within the wet plant populations there were also two biotypes. Innes (1990) found high interpopulational genotype variation in Polytrichum juniperinum Hedw., although variation within populations was low, indicating that mating occurs primarily among members of the same area and that gene flow distances are relatively short compared to other mosses with high variation within populations. High levels of genetic diversity have also been detected within and among populations of Sphagnum pulchrum (Braithw.) Warnst. with the highest genetic distance between populations at 0.42 (Daniels 1982).

Cummins and Wyatt (1981) were the first to determine the degree of genetic variability among individual moss plants within samples of a population. Atrichum angustatum (Brid.) B.S.G. was found to be electrophoretically polymorphic within and

among populations and within 5 X 5 cm samples. The degree of variability detected within and among populations was comparable to variabilities in angiosperms and animals. Meagher and Shaw (1990) found genetic variation within distinct clumps (ca < 60 cm^2) of Climacium americanum, although the majority of variation in this moss was among clumps. Probably the most interesting study in this area was done by Wyatt et al. (1987, 1989) in which levels of genetic diversity were detected in populations of Plagiomnium ciliare (C. Muell.) Kop. that were comparable to the vascular plants with the most highly recorded genetic diversities: the conifers (Ennos 1990). Not only did these workers find high levels of variation between and within populations, but they also found genetic heterogeneity in groups of five plants from 25 cm^2 samples of moss, although as of yet, there is no understanding how the genetic diversity of samples of populations relate to the genetic diversity of the population as a whole. Finally, Wyatt et al. (1989) found that there was more genetic diversity in mosses from old growth forests than in secondary growth forests indicating that a genetic bottleneck had probably taken place not too distantly in the past.

Evidently the theories that state that bryophytes have slow rates of evolution because they are depauperate in genetic variability must be rejected based on the above studies of electrophoretically detectable variation, and yet the fossil record suggests that mosses have not evolved as recently as most tracheophytes. What are the explanations for this apparent discrepancy? It has been suggested that the genes that are detected and quantifed through electrophoresis are selectively neutral and are not linked with genes which determine fitness, therefore while the electrophoretically detectable variation is high, the actual genetic variation involved in evolution may be low (Brown et al. 1989; de Vries et al. 1989; Dewey 1989; Ennos 1990; Nei 1988; Szweykowski 1984; Yamazaki 1981; Zielinski 1986). If the high allozyme heterogeneity detected in bryophytes describes genes which are not affected by natural selection, then we can conclude that the rate of directional

evolution in bryophytes is quite low as the evidence suggests. We can also conclude that the potential to evolve in bryophytes is evinced by high variation in some traits (Zielinski 1986), and we can conclude, although less securely, that natural selection is working to maintain bryophyte traits controlling fitness rather than to change them. Natural selection will select strongly against deleterious mutations, but if the mutations are selectively neutral they will remain in the population. If high electrophoretically detectable genetic diversity is selectively neutral and selected traits are relatively constant, centripetal or stabilizing selection is in action.

Other explanations for the high electrophoretically detectable genetic variability in bryophytes are based on mutation rates. Mutations of characters associated with fitness would be strongly selected against in haploid organisms, but mutations of selectively neutral traits may be retained in the population with no effect on the individual members. If electrophoresis detects only selectively neutral gene diversity, then a great deal of the variation may be due to mutation. Shaw (1990) found a substantial amount of variation in the morphology, germination percentage, gametophytic growth, and copper tolerance in Funaria hygrometrica Hedw. plants derived from the same genetic individual, indicating that mutation occurs often and at different stages in the development of the moss plant. Extremely high mutation rates have been detected in some plants; one in every 80 Y chromosomes per generation mutates for centromere relocation in Rumex acetosa L. (Parker and Wilby 1989). Furthermore, there is evidence that some mutations may in fact be biological responses to environmental stimuli, rather than simply random events (Eckhardt -Schupp 1989; Lenski 1989; and Roth et al. 1989). Finally, mutations may be particularly important in long-lived perennials, like some moss species, as each apical bud has more chance of undergoing mutation than in short lived species. Apical bud mutations lead to genetic diversity not only in the population, but also within the individual (Daniels 1982; Fahselt 1989; and Nickrent and Wiens 1989).

Alternatively, electrophoretically detectable genetic variation may be indicative of all genetic variation in the population or species. Some researchers suggest that bryophytes and other clonal organisms show high degrees of genetic variation because they have been naturally selected for by a very fine grained micro-habitat mozaic, and within each micro-habitat the genotypes are relatively homogenous (Cummins and Wyatt 1981; Daniels 1982; Dewey 1989; Ellstrand and Roose 1987; Spieth 1975; and Wyatt et al. 1989). Daniels found that populations of Sphagnum recurvum var. mucronatum (Russ.) Warnst. (1985a) and S. compactum DC. ex Lam. et DC. (1985b) were more genotypically complex in habitats that were variable in terms of water level and chemistry than in habitats that are relatively stable through time, indicating that a connection may exist between environmental selective pressures and electrophoretically detectable genetic variation. Genetic diversity may be caused through differential natural selection on different developmental stages; the moss protonema, no doubt, has different selective pressures acting on it than has the moss sporophyte (Dewey 1989; de Vries et al. 1983; and Zielinski 1986). Maravolo et al. (1967) found that the thallus and stalk of Marchantia polymorpha expressed different enzyme banding patterns from the antheridaphore disks.

The bands that are produced through electrophoresis are considered phenotypes which, theoretically, could be plastic in their response to the environment. Zielinski (1986) found that peroxidase and esterase banding patterns in Pellia endiviifolia differed among populations in the field, but when the same populations were cultured in the laboratory for two to six months the differences were not detected. Cronberg (1989) found allozyme differences in one enzyme system between Sphagnum capilifolium (Ehrh.) Hedw. and S. rubellum Wils., but he could not conclude that they were actually genetically different because the two species lie on either end of the mire-margin gradient and the electrophoretic phenotype difference may have been environmentally induced.

Also, high genetic variabilities in mosses could result from ancient or recent polyploidy (de Vries et al. 1989; and Szweykowski 1984). Plagiomnium ciliare is suspected of undergoing polyploidy long in the past and has since been silenced at a number of loci (Wyatt et al. 1989). Longton (1976) has suggested that the majority of mosses are autopolyploids which implies that the argument of mosses possessing low genetic diversity because of their dominant haploid state can be discarded in many cases as polyploidy allows for genetic buffering.

A final explanation for the unexpected high levels of genetic heterogeneity in bryophytes is that gene flow distances may be longer than expected. Spore numbers per capsule are so large (between several hundred thousand to two million or more (Longton and Miles 1982)) that if even only a very small fraction of the spores produced in one population was carried extrordinarily far, it could account for the genetic diversity found in another population (de Vries et al. 1983; and Wyatt 1982). Moss fragments may also have longer dispersal rates than we now know.

Most investigators have found that genetic distances among populations of bryopytes do not relate in any way to spatial distances. Such patterns can provide information on the history or evolution of a species (Crouau-Roy 1989). Dewey (1989) found no geographic arrangement in three genotypes of Riccia dictyospora. Innes (1990) found no relationship between genetic and spatial distances in populations in Polytrichum juniperinum and neither did Wyatt et al. (1989) in Plagiomnium ciliare, nor deVries et al.(1989) in Racopilum species. Speith (1975), however, found similarities between the patterns of genetic distance and the patterns of spatial distance only when he expanded the range of his studies. He concluded that in a small area the microhabitats in which Neurospora intermedia (a haploid fungus) occurs are more the same than different. Differing selective pressures are only evident over wide geographical ranges.

There are three objectives to the population genetics section of this study: 1) to quantify genetic diversity of M. triquetra and to relate the degree of variability to genetic diversity records in other mosses and organisms, 2) to determine whether genetic diversity in M. triquetra is related to latitude, and 3) to determine to what extent the genetic diversity of samples of M. triquetra represent the genetic diversity of entire populations and to examine this relationship with regards to latitude.

Corollary

High variation in a number of biological aspects, such as habitat, morphology, growth responses, and genetics, along an ecotone indicates local adaptation. Local adaptation, in turn, implies a potential to evolve. If Meesia triquetra, as a representitive moss, is highly variable along an arctic-boreal gradient, it may have a high evolutionary flexibility, although significant evolution and speciation in this moss (and possibly others) may be minimized by stabilizing natural selection.

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II. The habitat and distribution of Meesia triquetra in North America and Greenland.[1]

Introduction

Meesia triquetra (Richt.) Aongstr. can be distinguished from the other two North American species of Meesia by a distinct three-ranked leaf arrangement, acute leaf apices, denticulate leaf margins, and dioicous sexual condition.

Meesia triquetra is a rich fen indicator species of high fidelity. In the boreal region it grows in carpets in open mires, including the flarks of patterned fens and floating mats of pond margins. Meesia triquetra can also be found in hollows of alkaline, swampy Betula and Salix woods. In the Arctic, M. triquetra grows on calcareous seepage slopes and at the bases of hummocks in wet meadows. This moss is considered uncommon and strictly limited in its distributution by habitat availability (Odgaard 1988 and Slack et al. 1980). I had the opportunity to outline the habitat and distribution of this rare indicator species in North America as part of a larger work on the population biology of M. triquetra.

Meesia triquetra usually occurs in fens with high species richness. Among the most abundant moss species found in these fens are Aulacomnium palustre (Hedw.) Schwaegr., Bryum pseudotriquetrum (Hedw.) G.M.S., Drepanocladus revolvens (Sw.) Warnst., D. vernicosus (Mitt.) Warnst., and Tomenthypnum nitens (Hedw.) Loeske. It has also been found as isolated plants in carpets, below lawns of Sphagnum angustifolium (Russ.) C. Jens. and hummocks of S. magellanicum Brid., although this assemblage is rare. When present M. triquetra can be abundant, but is usually found as stems intermingled in carpets of Drepanocladus revolvens (Sw.) Warnst. and Scorpidium

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scorpioides (Hedw.) Limpr. Other indicator species of these mires are Calliergon trifarium (Web. and Mohr) Kindb., Catoscopium nigritum (Hedw.) Brid., and Cinclidium stygium Sw. The most abundant vascular plants found in fens occupied by M. triquetra are Betula pumila L., Carex species, Menyanthes trifoliata L., Potentilla palustris (L.) Scop., and Salix pedicellaris Pursh. (Chee 1988; Nicholson & Vitt 1990; and Slack et al. 1980).

In order to study the surface water chemistry of M. triquetra habitats, water samples were taken from fifteen fens in which Meesia triquetra occurs from boreal west-central Alberta, subarctic Yukon Territory, and from the High Arctic on Ellesmere Island during the summer of 1989. Water chemistry characteristics were analysed using the methods of Bierhuizen and Prepas (1985). These data, data from Janssens (1981), and unpublished data from W.-L. Chee and B.J. Nicholson (University of Alberta) are summarized in Table II-1.

Vitt and Chee (1990) found that poor, moderate-rich, and extreme-rich fens can be distinguished from one another on the basis of surface water pH, calcium and magnesium concentrations, and electrical conductivities. Surface waters in which M. triquetra grows are typical of moderate- and extreme-rich fens, characterized by high pH from 5.5 to 7.5, although M. triquetra has been found growing in water with pH as low as 4.7, and high electrical conductivities from 50 to 300 μS, however conductivities have been recorded as high as 1035 and as low as 12 μS. Calcium and magnesium concentrations in surface waters of fens in which M. triquetra occurs also are typical of rich fens; they range from about 30 to 60 mg L^{-1} and 6.0 to 20 mg L^{-1} respectively, although values as low as 0.8 mg L^{-1} for calcium and 0.3 mg L^{-1} for magnesium have been recorded. Other element concentrations are most often found in the following ranges: sodium 0.5 to 10 mg L^{-1}, and potassium 0.5 to 5 mg L^{-1}. Sulphate concentrations are extremely wide ranging from 0.0 to 447.4 mg L^{-1}, whereas chloride concentrations are limited between 0.1 to 22.5

Table II-1. Chemical characteristics of surface waters from fens in which Meesia triquetra occurs.

Characteristic	n	Mean	Standard deviation	Range
pH	61	--	--	4.7 - 8.1
Hydrogen ions per l ($x10^{-6}$)	61	1.5	3.3	0.0001 - 19.0
Ca (mg l^{-1})	31	34.4	25.9	0.8 - 117.0
Mg (mg l^{-1})	31	10.5	7.7	0.3 - 34.4
Na (mg l^{-1})	31	5.6	8.7	0.1 - 42.8
K (mg l^{-1})	31	1.7	2.9	0.1 - 5.8
SO_4 (mg l^{-1})	36	16.0	74.8	0.0 - 447.4
Cl (mg l^{-1})	14	4.2	6.1	0.1 - 22.5
Total phosphorus ($\mu g\ l^{-1}$)	15	77.2	85.6	1.6 - 322.7
Total dissolved phosphorus ($\mu g\ l^{-1}$)	14	7.1	3.0	1.6 - 11.2
NO_3-N ($\mu g\ l^{-1}$)	14	5.3	6.5	0.6 - 26.3
NH_4-N ($\mu g\ l^{-1}$)	14	18.3	21.4	0.1 - 66.5
Alkalinity (meq l^{-1})	15	166.7	65.6	47.5 - 329.9
Conductivity (microsiemens)	43	179.4	222.2	12 - 1035
Turbidity (nephlometric turbidity units)	14	27.7	18.9	7.5 - 60.0
Colour (mg platinum l^{-1})	14	10.4	7.1	0.3 - 28.0

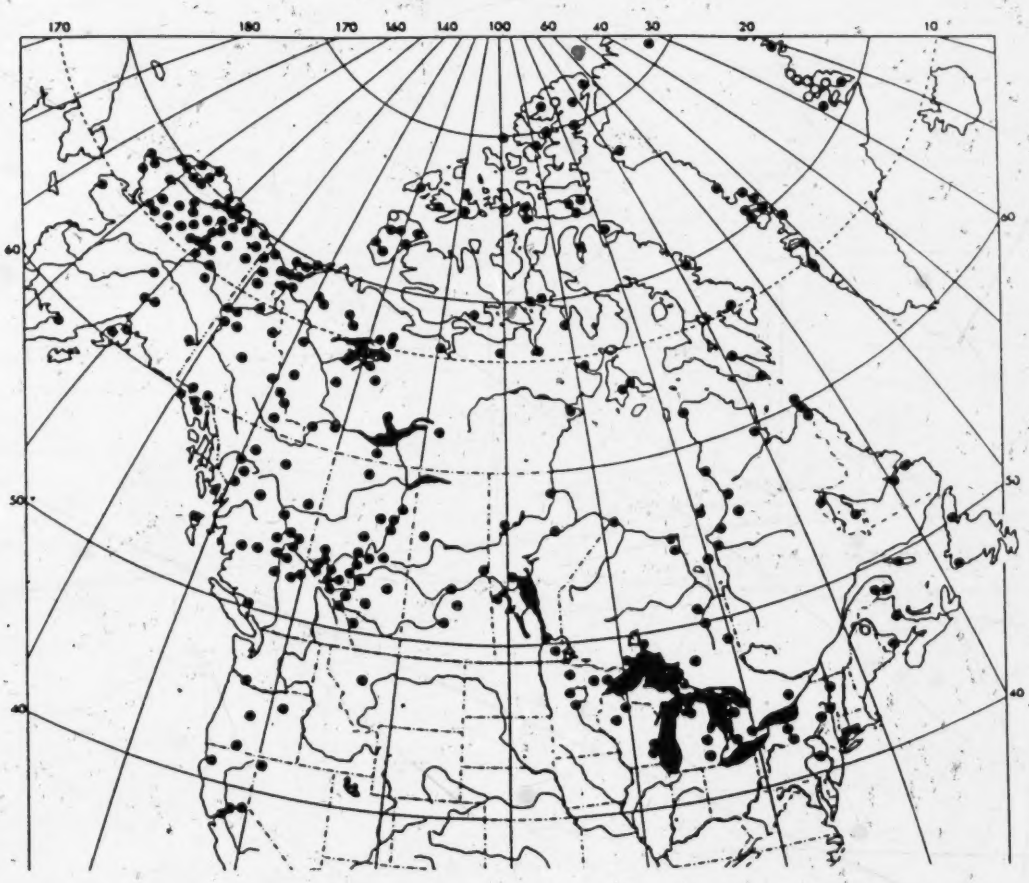
mg L^{-1}. Total phosphorus concentrations range from 1.3 to 322.7 µg L^{-1} with dissolved phosphorus at considerably lower levels. Nitrogen concentrations usually range from 0.6 to 26.3 µg L^{-1} for nitrate and 0.1 to 66.5 µg L^{-1} for ammonium. Alkalinity is high with a mean of 166.7 meq L^{-1}.

Meesia triquetra is a circumboreal moss. The world distribution includes Europe, from Spain north through France, the British Isles, Sweden, northern Norway, and east to Romania and northern European U.S.S.R. Meesia triquetra has been collected throughout the central and northern U.S.S.R. with the exception of the Kamchatka Peninsula and northernmost Krasnoyarsk. Elsewhere in Asia, collections have been reported from Mongolia, northeastern China, and northeastern India. A few specimens have been collected from the higher elevations of southeastern Australia, central Papau New Guinea, and western Venezuela (Abramova & Abramov 1976; Amann 1912; Frahm & Frey 1983; Gangulee 1974; Gao 1977; Husnot 1884-1890; Landwehr 1984; Nyholm 1975; Ochyra et al. 1988; Odgaard 1988; Podpera 1954; and Scott & Stone 1976).

The North American distribution of M. triquetra discussed here is based on specimens from ALA, ALTA, C, CAFB, CANM, COLO, DUKE, F, FH, IA, MICH, MIN, MO, MU, NY, NYS, NFLD, PENN, QFA, S, SFS, TENN, TRTC, UBC, WIS, and WTU. Over 1200 specimens were examined. In addition, Greenland sites from Holmen et al. (1974), Canadian arctic sites from Kuc (1973), and one Maine site from N.G. Miller (unpublished) are included (Fig. II-1). The North American distribution of fossil records from the Quaternary was determined from Baker et al. (1987), Janssens (unpubl. and 1981), and Miller (1980a) with additional records from unpublished data of P. Kuhry, N.G. Miller, and B.J. Nicholson.

North American collections of extant populations have been made from Alaska and the coast of British Columbia to Labrador and Newfoundland (Fig. II-1). The distribution of this species is from northern Ellesmere Island, south to northern California and

Fig. II-1. The distribution of Meesia triquetra in North America and Greenland. Open circles represent specimens cited in Kuc, 1973 and Holmen et al., 1974.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Montana in the west and Pennsylvania and Wisconsin in the east. A large number of collections have been made from the mountain ranges and foothills of Alaska, British Columbia, and Alberta; also notable are the many collections from the Great Lakes area. Calcareous bedrock underlies these regions. On Greenland, M. triquetra has been found mainly on the east and west coasts, north of the Arctic Circle.

Subfossil records from between 144 and 1,800,000 years B.P. (Baker et al. 1987; Janssens unpubl. and 1981; and Miller 1980a,) are located within the present day distribution of M. triquetra except for one record from southeastern Iowa, dated between 899 and 144 years B.P.and one record from southern Ohio, dated between 19,585 and 19,355 B.P. (Fig. II-2). Other subfossils of rich fen bryophytes have been found beyond their present day range. Miller (1980b) found subfossils of Scorpidium scorpioides (Hedw.) Limpr. and S. turgescens (T. Jens) Loeske. and Janssens (1983) found subfossils of Drepanocladus lycopodioides (Brid,) Warnst. and D. lapponicus (Norrl.) Smirn. south of extant populations of these species. Presumably the cooler climate during the Pleistocene enabled boreal mosses to colonize more southern regions. However, Janssens (1983) also found subfossils of D. crassicostatus Janssens and D. sendtneri (Schimp.) Warnst. north of their present day range. The Iowa and Ohio records of M. triquetra indicate that the range of M. triquetra extended farther south in the past, although only 400 km south of the nearest extant population.

Baker et al. (1987) used the Iowa specimen as evidence that Iowa experienced a period of climate cooling between 899 and 144 B.P. which roughly correlates to the "Little Ice Age" when glaciers in Alaska expanded. They also suggested that cultural eutrophication may have caused the vegetational change from rich fen to Typha marsh in their coring area. Cultural eutrophication, drainage, and industrialization have reduced the number of sites in which M. triquetra is found in Europe (J.-P. Frahm, pers. comm.). The same environmental pressures may well be affecting fens in North America. Thus,

Fig. II-2. The distribution of Quaternary subfossil records of Meesia triquetra in North America based on Miller, 1980a; Janssens, 1980 and 1981;and specimens from ALTA.

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the disappearance of M. triquetra from Iowa may be due to effects which are cultural rather than climatic. Several of the herbarium specimens documented in this study were over 100 years old and some of them were collected from areas which are now well developed and heavily populated. I suspect that the actual present day range of M. triquetra is restricted to relatively undisturbed areas as its rich fen habitat is easily modified, in particular the surface water chemistry of these fens is sensitive to climatic and anthropogenic influences. Hopefully, these areas will be protected so that the rich fen bryoflora will not reach near extinction in North America as it has in Europe.

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III. The chemical ecology of Meesia triquetra in western and northern Canada.

Introduction

In her 1982 work on bryophytes in relation to niche theory, Slack defined the realized niche as the ecological space in which a species can exist limited by physiological factors. Surface water chemistry is part of a complex set of environmental parameters which define the niches of mire species. For instance, Vitt and Slack (1984) found that pH, and calcium and magnesium concentrations are important in niche separation in Sphagnum, while Gignac (1990) found that climatic factors, conductivity, manganese, potassium, and height above the water table were also important.

Mire water chemistry has also been extensively studied in relation to mire vegetation and classification. Bogs and fens lie on a gradient of increasing pH, conductivity and cation concentration from ombrotrophic bog to minerotrophic extreme rich fen (Schwintzer and Tomberlin 1982; Sjors 1961; Slack et al. 1980; and Vitt and Bayley 1984). Gorham and Pearshall (1956) stated that conductivities are usually above 70 microsiemens in fens and below 70 microsiemens in bogs, and that nutrient levels are higher in fens than in bogs, however Swintzer and Tomberlin (1982) and Vitt et al. (1975) have found that nutrient levels (nitrogen and phosphorus) in fens can be lower or equal to those in bogs and the latter group have suggested that it is the water flow which regulates nutrients and not necessarily the concentration of nutrients in the water.

No particular bryophyte species distributions have been directly linked to environmental parameters (Brown 1982), but various studies have been made to determine indicator species and species assemblages associated with particular environments (Vitt and Slack 1984). For example, the bryophyte vegetation in streams of the Canadian Rocky Mountains was statistically separated into different associations on the basis of

calcium and magnesium concentrations as well as soil texture and water level (Vitt et al. 1986). The species compositions of peatlands in the Netherlands have changed due to decreases in calcium concentrations in the surface water which indicates the sensitivity of peatland species to water chemistry (Wassen et al. 1989).

Water chemistry can have substantial effects on the morphology and growth of moss species. Rhynchostegium riparioides (Hedw.) Card. varies in size, leaf length, leaf shape, and denticulation along a gradient from calcareous head waters and springs to large rivers with high nutrient concentrations (Wehr and Whitton 1986). In the laboratory, Austin and Weider (1987) found that elevated levels of hydrogen ions, nitrate, ammonium, and sulphate affected the growth and chlorophyll content of three Sphagnum species, and that the response was species dependent. Ferguson et al. (1984) have suggested that the decline of Sphagnum bogs in the South Penines, U.K. and the failure of transplants there is due to elevated nitrogen and phosphorus levels in addition to elevated sulphur levels in precipitation.

Slack (1982) stated that the realized niche can change from locality to locality because of the changing demands on the physiology of the species in question. This study examines the variation in surface water chemistry of fens in which Meesia triquetra (Richt.) Aongstr. occurs along an arctic-boreal gradient, to determine whether the chemical aspect of the niche of this moss changes over a wide range of macroclimates.

Methods

Study regions

Three regions were designated over a Canadian Arctic-Boreal gradient: one from Boreal, Alberta, one from the forest tundra in the Yukon Territory (subarctic), and one from the High Arctic on Ellesmere Island, N.W.T. The subarctic region is approximately half way between the Boreal and Arctic sites.

The Boreal region is located between Edson and Nordegg, Alberta along Highway 47, Highway 40, and the Cardinal River Road (between 55° 35' N 116° 26' W and 52° 50' N 116° 05' W). This is a wooded area of the Alberta plain at the eastern edge of the Rocky Mountain foothills. It is underlain by Tertiary sandstones and shales, with a cover of hummocky ground moraine deposited by the Cordillerian glacier during the Wisconsinan period. The till is stoney with limestone blocks (Clayton et al. 1977a). Elevations rise between 1200 and 1800 m above sea level (Drinkwater et al. 1969). This area is also part of a sand dune complex formed by glacial Lake Edson (Slack et al. 1980).

The climate of the Edson-Nordegg area is temperate with a July mean monthly temperature of 14.4°C. It has a frost free period (number of days between the last frost in the spring and the first frost in the fall) of approximately 80 days and it receives an average annual precipitation of 533 mm, with 305 mm falling during the frost free period (Alberta Environment 1988; and Drinkwater et al. 1969).

Tree covered hills; mainly dominated by Picea glauca (Moench) Voss, P. mariana (Mill) BSP., and Pinus contorta Loudon associations and occasional Populus tremuloides Michx. stands alternate with abundant ponds and open mires in low-lying areas (Clayton et al 1977a; Drinkwater et al.1969; Slack et al. 1980).

Five fens were selected from this area. One was located along a pond margin, five km south of highway 16, on the east side of highway 47 (Plate III-1), two were in small basin fens (one on the west side of the Forestry Trunk Road, five km south of Pembina River crossing, and the other on the south side of the Cardinal River Road, 10 km west of the junction with the Forestry Trunk Road), and two were part of larger peatland complexes (one on the west side of highway 40, 15 km south of Robb, 1 km south of a provincial campsite, and the other on the west side of the Forestry Trunk Road, 10 km southeast of the junction with the Cardinal River Road).

Plate III-1. Pond margin fen near Edson, Alberta in which Meesia triquetra occurs.

The subarctic region is located along the Dempster Highway between Kilometers 141 and 197 (between 64° 30' and 65° 30'N at approximately 138° 50' W). The Dempster Highway is the link between Dawson City, YT. and Inuvik, N.W.T. It runs along river valleys and hill crests of unmanaged crown land.

The section of Highway used in this study runs over the Porcupine Plateau which consists of sedimentary bedrock of Paleozoic carbonates. The Plateau lies between the Richardson mountains to the northeast and the Ogilvie mountains to the southwest. Elevations range from 500 to 1000 m above sea level in rolling hills. Soils are humid, stoney or sandy aluvial deposits and glaciofluvial till. This region remained unglaciated throughout the Pleistocene (Clayton et al. 1977b).

The climate of this area is substantially cooler than that of the Edson-Nordegg area, with mean monthly temperatures in the negative twenties in January and of approximately 14°C in July. Annual precipitation is about 350 mm. The average annual frost free period lasts 60 days (Alberta Environment 1988; and Bryson and Hare 1974).

The vegetation on the Porcupine Plateau is forest tundra; alternating stands of stunted Picea glauca and P. mariana forests, and large stretches of open tundra. Forested mires have developed on poorly drained areas underlain by permafrost (Stanek et al. 1981; and Kojima and Brooke 1985).

Five fens were chosen for study on the Porcupine Plateau. One was along a pond margin at km 141, on the east side of the Dempster Highway, one was located near a wide-spread stream in the open tundra at km 96 on the west side of the Dempster Highway, one was located in a swampy Betula-Salix stand at km 190 on the east side of the Dempster Highway, and the other two were located in small basins adjacent to treed areas (one at km 175 on Dempster Highway (Plate III-2), and the other at km 183 on the west side of the Dempster Highway).

Plate III-2. Basin fen near the Dempster Highway, Yukon Territory, in which Meesia triquetra occurs.

The third region is located at Princess Marie Bay on Ellesmere Island, N.W.T. (79° 29' N, 75° 47' W). The base camp was five km from the coast in an estuary lowland which expands north for 20 km and was 5 km wide. The lowland is banked on either side by folded mountains of sedimentary limestones and sandstones laid down in the Ordovician and Silurian periods. The area was glaciated during the Pleistocene and experienced postglacial marine submergence. Isostatic uplift is still occurring at a substantial rate (Williams et al. 1980). All fens were located between 15 and 50 M above sea level.

Soils in this area are mainly poorly developed regosols of humid loamy glacial till or fluvial deposits (Clayton et al.1977b).

Climate studies of the Princess Marie Bay area are few. The limited records show mean monthly July temperatures of 6.6°C, a frost free period of 37 days (Williams et al. 1980) and the total precipitation for the months of July and August of 26.1 mm (G. Henry unpubl. data). The Princess Marie Bay lowland is considered a polar desert .

The vegetation of Princess Marie Bay is controlled, in the most part, by soil moisture. The land ranges from barren, or near barren, clay badlands, exposed rock and scree occasionally colonized by Dryas integrifolia M. Vahl, Saxifraga oppositifolia L., and Salix arctica Pall., to slightly more vegetated stable terraces which have in addition to the above species, species of Carex, Lesquerella, and Braya. Species richness and vegetative cover is highest along seepage slopes and in wet sedge meadows in low lying areas.

The five fens in this region were located within 15 km of each other. Two of the fens were located on patterned outflows of ponds (one on the east side of lowland, one km north of the coast, and the other on the east side of lowland, on a 15 m terrace, six km north of the coast), two were located in wet meadows (one was the most extensive meadow in lowland, seven km north of the coast (Plate III-3), and the other is between a large hill and the coloured mountain, 16 km north east of coast.), and the last was located

Plate III-3. Extensive fen at Princess Marie Bay, N.W.T., in which Meesia triquetra occurs.

along a gently inclined seepage slope on east side of lowland, on a 10 m terrace, six km from coast.

Water collection

Surface water was collected at the 15 fens. Two 250 ml polystyrene bottles and one 250 ml nalgene bottle were filled at each fen except on the seepage slope at Princess Marie Bay where only one of each type of bottle was used. All water samples were taken and analysed during the summer of 1989. The water was collected as close as possible to the dates when water quality analysis could be done. Samples were kept in cool storage between collection and analysis. The water at Princess Marie Bay was collected July 22 and 23 and analysed from July 27 to July 31, 1989. The samples from the subarctic were collected August 19 and 20, and the samples from the Edson-Nordegg area were taken August 25. Samples from these two areas were analysed between August 28 and September 2.

Water quality analysis

Fifteen water quality variables were measured in the surface water collected from each of the 15 fens after the methods of Bierhuizen and Prepas (1985). Total phosphorus and dissolved phosphorus concentrations were measured on a Mitton Roy spectrophotometer after acid digestion. Ammonium and nitrate concentrations were measured on a Technicon autoanalyser II. Cation concentrations of sodium, potassium, calcium, and magnesium, were determined through atomic absorption spectrometry. Sulphate and chloride concentrations were measured with a Dionex chromatograph. pH was measured in the field with a portable Extech pH meter. Alkalinity was measured in the laboratory, as were water colour, turbidity and conductivity.

Data analyis.

The data were analysed with univariate and multivariate techniques to determine whether the surface water in which Meesia triquetra grows varies over an arctic-boreal gradient.

First, regression analysis was performed on each variable against the latitude of the region. Second, Kruskal-Wallis analyses of variance were performed on each of the water quality variables to determine whether any of the variables vary significantly among regions. This non-parametric test was chosen because of the nature of the data. Since only 15 sites were chosen, the probability of the variables falling into normal distributions, or even distributions which could successfully be transformed into normal distributions, was low. However, parametric tests were used in the data analysis because the tests were considered sufficiently robust. Nonetheless, the results of the parametric tests should not be accepted without a certain degree of caution.

Third, a multivariate analysis of variance (MANOVA) was performed to determine whether there are overall significant differences among the three regions. Only 11 of the 15 variables were used in the MANOVA to allow for sufficient degrees of freedom. An arbitrary decision was made as to what four variables would be dropped from the analysis. Magnesium and sulphate concentrations were not used because they were found to be highly correlated to conductivity (correlation coefficients of 0.94 and 0.78 respectively). Other variables such as calcium concentrations and alkalinity were also highly correlated to conductivity but they were considered to be too ecologically important to drop from the analysis. Neither chloride nor potassium concentrations varied substantially between sites and both are relatively constant in fen ecosystems so they were also dropped from the analysis.

Finally, a principal components analysis was used to ordinate linear combinations of all 15 water quality variables for each site in multidimensional space. The ordination of these site scores was then reduced to two dimensional space on the first and second

principal components. Also the site scores were regressed against latitude to determine whether overall water chemistry varies with latitude. Principal components analysis was considered an appropriate ordination technique for this analysis because it treats data as if they were to increase or decrease linearly along a gradient, rather than in a Gaussian fashion, which is what I would expect of chemical data along a latitudinal gradient. Water from one of the Princess Marie Bay sites was not used in this analysis because all water chemistry variables were not available for this site.

Results

The water quality values for each of the 18 variables are listed in Appendix 1 and illustrated in Figure III-1. Means, standard deviations and coefficents of variation of all the water chemistry variables are listed in Table III-1. Sulphate concentration has the highest coefficient of variation at 2.92, while total phosphorus, nitrate, ammonium, and chloride concentrations are intermediate (above 1.00), and the coefficient for pH is lowest at 0.04.

Of all the variables, only total dissolved phosphorus, turbidity, and pH varied significantly with latitude in the regression analysis; the first two variables decreasing and the latter increasing over the gradient (Table III-2).

Alkalinity, turbidity, and total phosphorus, total dissolved phosphorus, nitrate, sulphate, and chloride concentrations were found to be significantly different at the 0.05 level among regions through the Kruskal-Wallis analysis (Table III-2).

The MANOVA indicates significant differences among regions only in total phosphorus, total dissolved phosphorus, pH, and turbidity (Table III-2). Although Pillai's Trace (SAS Institute Inc. 1982) is significant at the $p < 0.05$ level indicating that there are significant differences in the overall surface water chemistry among the three regions, Wilks' Criterion (Rao 1973) is not significant.

Fig. III-1. Surface water quality values for 18 variables in 15 fens in which Meesia triquetra occurs from three ecoclimatic regions: 1) High Arctic, 2) Yukon, 3) Boreal.

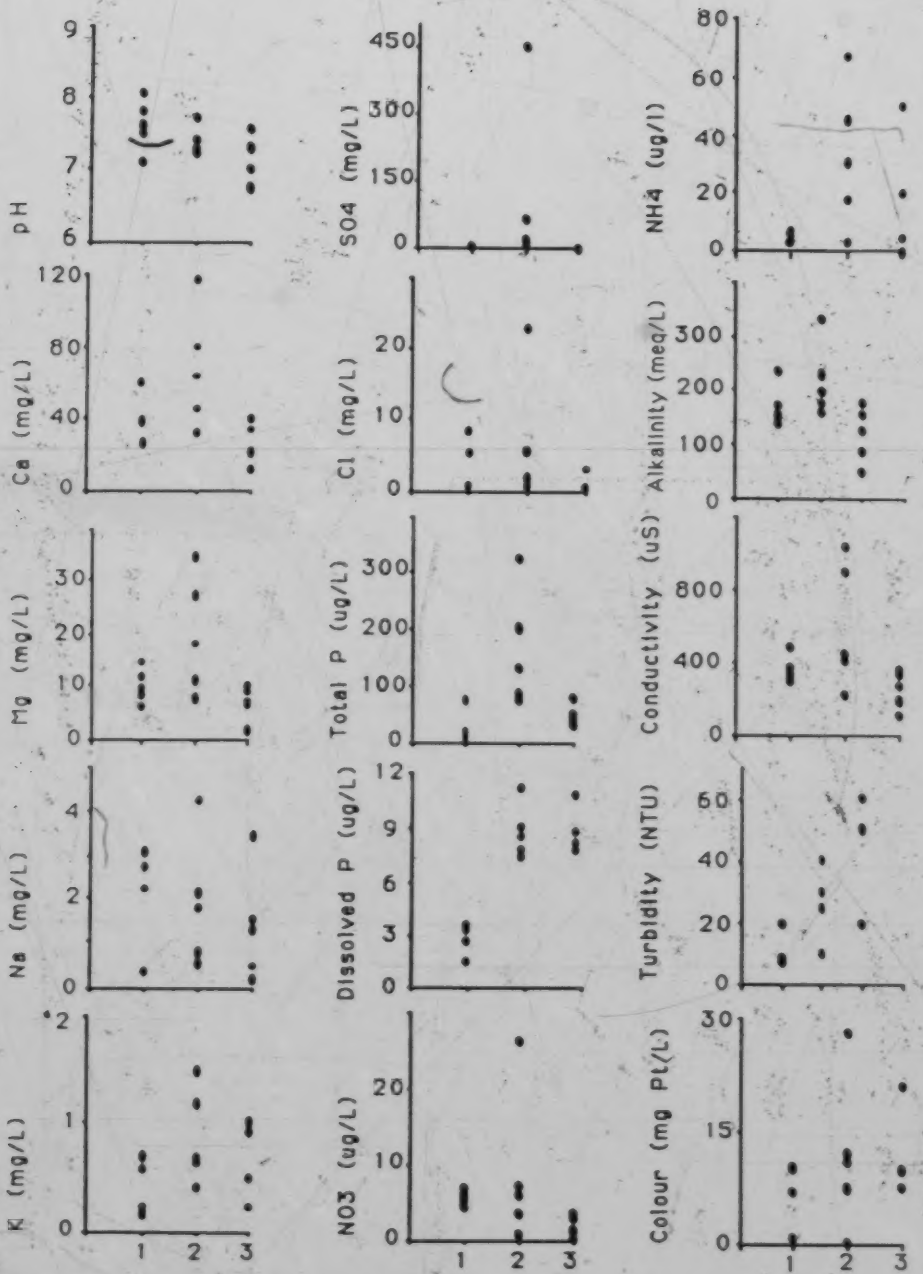

pH
SO4 (mg/L)
NH4 (ug/l)
Ca (mg/L)
Cl (mg/L)
Alkalinity (meq/L)
Mg (mg/L)
Total P (ug/L)
Conductivity (uS)
Na (mg/L)
Dissolved P (ug/L)
Turbidity (NTU)
K (mg/L)
NO3 (ug/L)
Colour (mg Pt/L)
1
2
3
Ecoclimatic Regions

Table III-1. Means and variances of surface water chemistry variables of fens in which Meesia triquetra grows. Coefficients of variation are expressed as percents.

Variable	n	Mean	Standard deviation	Coefficient of variation
Total Phorphorus ($\mu g \cdot L^{-1}$)	15	77.19	85.6	1.11
Total dissolved phosphorus ($\mu g \cdot L^{-1}$)	14	7.1	3.0	0.42
NO_3-N ($\mu g \cdot L^{-1}$)	14	5.3	6.5	1.23
NH_4-N ($\mu g \cdot L^{-1}$)	14	18.3	21.4	1.16
Na ($mg \cdot L^{-1}$)	15	1.8	1.3	0.72
K ($mg \cdot L^{-1}$)	15	0.6	0.4	0.67
Ca ($mg \cdot L^{-1}$)	15	45.3	26.1	0.58
Mg ($mg \cdot L^{-1}$)	15	12.2	8.1	0.66
SO_4 ($mg \cdot L^{-1}$)	14	40.5	118.3	2.92
Cl ($mg \cdot L^{-1}$)	14	4.2	6.1	1.45
pH	15	7.4	0.3	0.04
Alkalinity ($meq \cdot L^{-1}$)	15	166.7	65.6	0.39
Conductivity (μS)	15	402.3	250.6	0.62
Turbidity (nephlometric turbidity units)	14	27.7	18.9	0.68
Colour (mg platinum $\cdot L^{-1}$)	14	10.4	7.1	0.68

Table III-2 Regession of surface water quality variables of fens in which Meesia triquetra grows against region latitude.

Variable	n	r^2	Significance		
			Regression	Kruskall-Wallis	MANOVA
Total phosphorus ($\mu g \cdot L^{-1}$)	15	0.012	NS	**	*
Total disolved phosphorus ($\mu g \cdot L^{-1}$)	14	0.608	**	*	***
NO_3-N ($\mu g \cdot L^{-1}$)	14	0.072	NS	*	NS
NH_4-N ($\mu g \cdot L^{-1}$)	14	0.025	NS	NS	NS
Na ($mg \cdot L^{-1}$)	15	0.080	NS	NS	NS
K ($mg \cdot L^{-1}$)	15	0.146	NS	NS	--
Ca ($mg \cdot L^{-1}$)	15	0.019	NS	NS	NS
Mg ($mg \cdot L^{-1}$)	15	0.026	NS	NS	--
SO4 ($mg \cdot L^{-1}$)	14	0.002	NS	**	--
Cl ($mg \cdot L^{-1}$)	14	0.128	NS	*	--
pH	15	0.036	*	NS	*
Alkalinity ($meq \cdot L^{-1}$)	15	0.338	NS	*	NS
Conductivity (μS)	15	0.034	NS	NS	NS
Trubidity (nephlometric turbidity units)	14	0.61	**	*	**
Colour (mg platinum $\cdot L^{-1}$)	14	0.068	NS	NS	NS

*, $p < 0.05$; **, $p < 0.005$; ***, $p < 0.0005$

Principal components 1 and 2 account for 31.8% and 18.9% of the variation found in the data respectively. The first component is related to calcium and magnesium concentrations, and conductivity levels (eigenvector elements of 0.44, 0.44, and 0.45 respectively) and the second component can be related to nitrate concentrations and negatively related to colour (eigenvector elements of 0.37 and -0.45 respectively) (Table III-3). There is little separation among regions along the first principal component (Fig. III-2). Arctic and Boreal sites lie closer to the right but there is overlap with the subarctic sites. Subarctic sites have a large range over the second principal component; whereas, the Arctic and Boreal sites are well separated and lie in very narrow ranges. Neither first nor second principal component site scores are significantly related to latitude.

Discussion

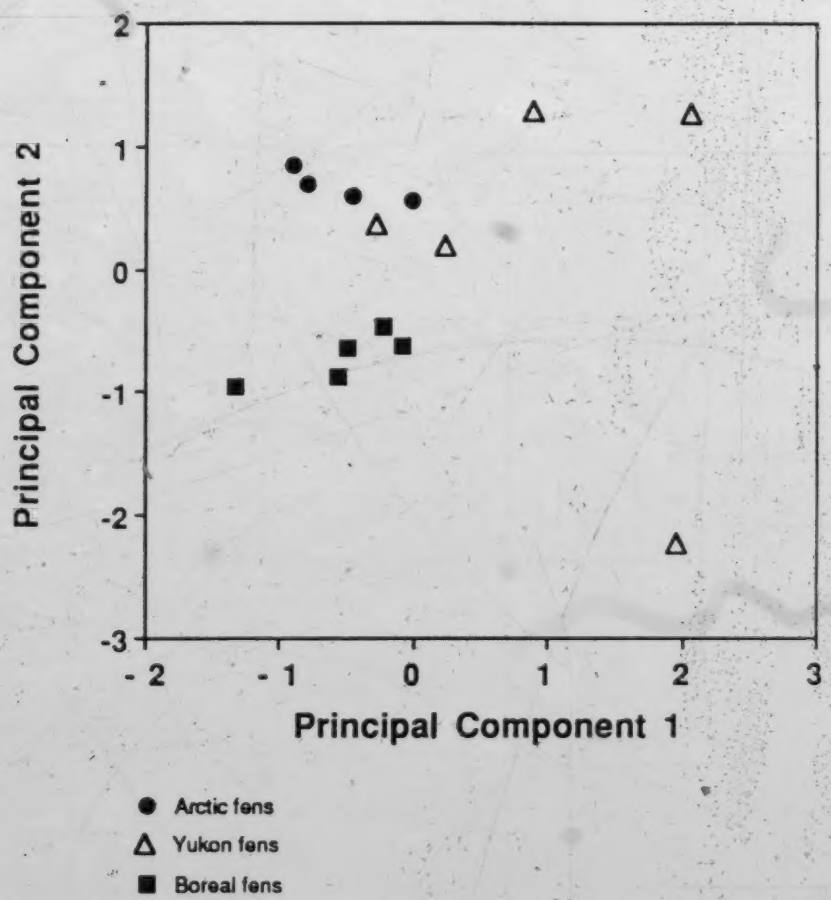
A major factor influencing this study, besides latitude, was the drought experienced in the Yukon during the summer of 1989. The fens were so dry that it was often difficult to find a pool deep enough to collect water from, and the Meesia triquetra plants were dehydrated to the point of contortion. Doubtless this had an effect on the water chemistry in the area. I suspect that this is the cause of the high coefficients of variation in many of the ion concentrations especially sulphate concentrations, and that this natural phenomenon is responsible for the ordination of sites along the first principal component.

The coefficent of variation in pH was very small which implies that M. triquetra has a very limited range with regards to pH. This moss is rarely found in waters with a pH above 8.0 or below 6.6 although it has been found in waters with pH as low as 4.6 (Nicholson 1987). This corresponds to Vitt and Slack's comment (1984) that M. triquetra is an indicator species of rich fens and Sjors' comment (1961) that rich fens are characterized by pH greater than 7.0. Although this moss appears to be able to survive in

Table III-3. Eigenvector elements of principal components 1 and 2 for surface water chemistry of fens in which Meesia triquetra occurs.

Water Chemistry Variable	Principal Component	
	1	2
Total Phosphorus	0.20	0.19
Total disolved phosphorus	0.16	-0.19
NO_3	0.13	0.37
NH_4	0.30	0.09
Na	-0.08	0.14
K	0.23	0.09
Ca	0.42	-0.09
Mg	0.39	-0.11
SO4	0.30	-0.34
Cl	0.20	0.32
pH	0.02	0.29
Alkalinity	0.34	0.33
Conductivity	0.42	-0.06
Tubidity	0.09	-0.34
Colour	0.06	-0.45

Fig. III-2. Principal components analysis of surface water variables of fens in which Meesia triquetra occurs.


Principal Component 2
2
1
0
-1
-2
-3
- 2
- 1
0
1
2
3
Principal Component 1
Arctic fens
Yukon fens
Boreal fens

waters with high nitrogen, sulphate, and chloride concentrations for at least one season (Fig. III-1), it is not obvious whether it would be able to continue to survive in mires with such concentrations for many consecutive years.

The regression analysis results should be examined with some caution because only three points were used on the independent variable axis. Phosphorus concentrations, turbidity, and pH varied significantly with latitude in the regression analysis; the first two variables decreasing and the latter increasing over the gradient. The source water for fens at Princess Marie Bay comes directly from glaciers no more than 15 km away. This short travelling distance and the fact that production and decomposition rates are low in the Arctic explains why the water there is clear and has low phosphorus concentrations. This source water also runs over bare limestone which would buffer the water against any organic acids which might tend toward lowering the pH and the limestone bedrock may in fact raise the pH slightly above neutral. This also explains the significant differences found in turbitidy and pH in the MANOVA and Kruskall-Wallis analysis.

Significant differences in total phosphorus, total dissolved phosphorus, nitrate, sulphate, chloride concentrations, and alkalinity can all be attributed to extremely high levels in the subarctic sites due to the drought. The MANOVA appears to be less sensitive to outlier values than the Kruskall-Wallis analysis. For example, in sulphate and nitrate concentrations only one value out of five appears to have separated the Yukon samples from the arctic and boreal samples in the Kruskall-Wallis analysis (Fig. III-1). These outliers are not sufficient to lead to significant differences in the MANOVA. However, a significant difference in pH values among sites was detected in the MANOVA which was not detected in the Kruskal-Wallis analysis. Either test would be more believable if the sample sizes were larger. What can be gained from these analyses is that the majority of the water quality characters do not substantially differ from fen to fen along an arctic-boreal gradient.

Although, the MANOVA detects multivariate differences in the overall water chemistry among regions and the PCA ordination also indicates that there are differences in water chemistry among the regions, it is evident that the Yukon water samples are substantially different in terms of variation and range from the arctic and boreal samples. I suggest that the multivariate differences detected by the MANOVA are due to the drought in the Yukon and its effect on water chemistry rather than actual differences in mire character. Furthermore, the regression analysis of PCA site scores indicates that there is no variation in water quality with latitude. A comprehensive study of water quality among fens should be done over several years to limit the variation due to rare annual events. It would also be advantageous to sample several times over the season at each region to determine seasonal variation among mires.

In conclusion, this study has defined the narrow habitat requirements for Meesia triquetra. A range of values for many water quality characteristics of the fens in which M. triquetra occurs have been recorded and now can be compared to those of other mire species to discuss niche breadth and indicator species characteristics. Since the majority of water quality variables do not substantially differ from fen to fen, the chemical aspect of the realized niche of M. triquetra many be fairly constant over an arctic-boreal gradient despite the changing demands on the physiology of this moss throughout its range.

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IV. Patterns of morphological variation in the brown moss Meesia triquetra over an arctic-boreal gradient. [1]

Introduction

Morphological variation

Morphological variation in plants, due to genotypic variation and phenotypic plasticity, can enable species distributions to expand, thereby exposing populations to new selective pressures (Longton 1979 and Stearns 1989). These new selective pressures can lead to further variation and possibly speciation. Each morphological character in a plant is associated with a plasticity character which varies as a function of environmental signals and is genetically controlled, thus subject to natural selection (Bradshaw 1965; and Stearns 1989). In fact, morphological trait means, and the amount and patterns of plasticity among individual congeners are independent of one another during the evolutionary process, which indicates that all three characteristics are directed by separate selective pressures (MacDonald and Chinnappa 1989). Phenotypic plasticity may or may not result in adaptive advantages such as increased survival, reproduction, or growth of an individual. A plant not physiologically buffered against environmental stresses will respond in a non-adaptive plastic fashion, such as reduced production or fertility (Schlichting 1986). Bryologists have argued for decades whether the evolution of bryophytes has been arrested at a primitive stage (Steere 1958) or whether bryophytes possess a relatively high potential to evolve (Longton 1976 and Wyatt et al. 1989). Morphological variation may be used as an indicator of phenotypic plasticity, genotypic variation, and of evolutionary potential in the long-standing debate on the rate of evolution in bryophytes.

- 1. A version of this chapter has been submitted for publication. Montagnes and Vitt 1991. Systematic Botany.

It is well known that some bryophytes exhibit morphological variation (Longton 1979b; and Schofield 1981). Isothecium stoloniferum Brid. is nearly dendroid when growing on the bases of tree trunks, but is distinctly pinnate in humid open forests, and pendent when found on branches and trunks in humid closed forests (Schofield 1981). The Macrocoma tenue-M. sullivantii complex varies in leaf and cell length throughout its distribution in the Americas, Africa, Asia, and the South Pacific (Vitt 1981). Rhychostegium riparioides (Hedw.) C. Jens varies in plant size, leaf dimensions, and the degree of leaf denticulation along a gradient from head waters with low nutrient concentrations to large rivers with high nutrient concentrations (Wehr and Whitton 1986). Glime and Raeymaekers (1987) found that species of Fontinalis varied in branch production along a temperature gradient. Vitt and Horton (1976) found patterns of variation in leaf shape in North American Climacium americanum Brid. and C. dendroides (Ren. et Card.) Grout which followed a northwest-southeast gradient from Alaska to Florida. Three Schlotheimia species varied along a latitudinal gradient from 10° to 60° S in Australia and New Zealand. Schlotheimia brownii Schwaegr. varied in cusp length, while S. knightii C. Meull. and S. campbelliana C. Meull. varied in cell length parameters. Each of these three congeners exhibited different patterns of morphological variation (Vitt 1989).

The latitudinal gradient

The environmental gradient from temperate to polar regions has long interested plant ecologists both for community study and autecology. The length of this gradient and its complexity give ample opportunity to study plant responses to environmental stimuli. Arctic adaptations in vascular plants have been well documented (Bliss 1962; Chapin 1983; Corbet 1969; Love and Love 1974; and Savile 1972). The arctic climate is characterized by a short, cold growing season, strong winds, low light intensity, low

precipitation, and the long arctic day coupled with the equally long arctic night. Low nutrient availability, caused by low decomposition rates and slow soil forming processes, is an indirect effect of the harsh climate. Despite low temperatures, arctic environments experience fewer freeze/thaw cycles per year than temperate regions because of the long photoperiod, which helps to ameliorate the climate (Corbet 1969). In addition, the arctic climate is more variable with respect to precipitation, mean summer temperatures, and wind speeds from year to year than temperate climates (Addison and Bliss 1980; Bliss 1962; Bliss et al. 1973; Savile 1972; and Warren Wilson 1966).

Temperature is the primary factor affecting growth in arctic vascular plants; in general, carbon gain is low. Leaves are usually smaller in arctic members of wide ranging species. Weilgolaski (1980) suggested that smaller leaves have less risk of frost damage. Warren Wilson (1966) found that the net assimilation rate, relative growth rate, and the leaf area ratio of three forbs decreased substantially from temperate climate in England to the mid-Arctic on Cornwallis Island, N.W.T. He stated that low temperatures reduce the rate at which assimilates are used in respiration and new growth, which results in an accumulation of sugars, which in turn results in a decrease in assimilation.

Most arctic plants have adopted a short cushion growth form which reduces heat and water loss, protects against wind abrasion, and takes advantage of the relatively high temperatures at ground level (Addison and Bliss 1980; Bliss 1962; Longton 1988a; and Savile 1972). Bryophytes have probably not adapted their growth form to the Arctic environment, but rather are predisposed to life in the Arctic by their small stature (Longton 1988b).

Few comprehensive studies have been made on morphological variation in bryophytes along latitudinal gradients. Hylocomium splendens (Hedw.) B.S.G. exhibits striking morphological variation from temperate to arctic habitats. Hylocomium splendens ssp. giganteum Pers. ex Vitt, found in the west coast of Canada, grows in wefts and

possesses the characteristic "stair-step" frond; whereas variety obtusifolia (Geh.) Par., found north of treeline, lacks this character. The variety splendens is intermediate to giganteum and obtusifolia in many characters.

Longton (1974) found that Polytrichum strictum Brid. decreased in its annual growth increment length and weight, the number of leaves per annual growth increment, and leaf length along latitudinal gradients from the tropics to the extreme polar locations of Galindez Island (65° 15' S) and Rankin Inlet, N.W.T. (62° 45' N). He determined experimentally that these differences were controlled both endogenously and exogenously. Longton (1979a) suggested that P. strictum is widespread because of its ability to adapt morphologically to a variety of environments both genetically and through phenotypic plasticity. Vitt (1991), on the other hand, found no significant correlation between annual growth increment length and latitude in P. strictum along a gradient from 49° to 76° N. Longton's southern specimens were collected from Manitoba, while Vitt's southern specimens were collected from Alberta. It has been suggested that the discrepancy between these two studies exists because the mean summer temperature in Alberta is lower than that of Manitoba (Vitt pers. comm.).

Longton (1981) grew populations of Bryum argenteum Hedw. collected from polar, temperate, and tropical localities and found that morphological variation among the populations, in particular in the antarctic population in contast with the others, decreased substantially in a common garden experiment.

Study species

Meesia triquetra (Richt.) Aongstr. was considered an excellent subject for a detailed study on patterns of variation along an Arctic-Boreal gradient because it putatively possesses innate annual growth markers and has a wide distribution in North America ranging from northern Alaska and northern Ellesmere Island, N.W.T. in the high arctic south to

northern California and Montana in the west and Pennsylvania and Wisconsin in the east. The gradient covers 44 degrees of latitude and a continuum of macroclimates. This brown moss is an indicator species of moderate to extreme rich fens. It grows erect in carpets of Drepanocladus revolvens (Sw.) Warnst. and Scorpidium scorpioides (Schimp.) Limpr. The object of this study is to quantify the morphological variation in M. triquetra over an arctic-boreal gradient and to relate the degree of morphological variation in this moss to its potential for evolution.

Materials and Methods

Morphometrics

One hundred and nine herbarium specimens collected from North American fens (Fig. IV-1) were examined for 11 morphological characters (Table IV-1). Three stems of at least three years of age were taken from each specimen. The stems were rehydrated in boiling water before they were measured. It was assumed that the innate growth markers were produced annually. The length of the penultimate growth increment was measured with calipers to the nearest tenth of a millimeter. The number of leaf whorls per growth increment, and the number of whorls per cm were recorded. The growth increment was cut from the stem and dried at 25°C for at least 24 hours. Dry weight of the growth increment was recorded, giving the amount of growth in milligrams per year. The weight per millimetre of growth was determined for each of the three stems per sample.

Leaves from the current season of growth from each stem were removed from the stem and mounted in Hoyer's solution (Anderson 1954) as permanent mounts. Each mount contained leaves from only one stem. If all the leaves in the final growth increment were immature, leaves from the growing season before the penultimate season were mounted.

Fig. IV-1. Ecoclimatic region boundries and collection locations of Meesia triquetra specimens used in the morphometric analysis.

170
180
170
160
140
100
80
60
40
30
20
10
60
50
40
High Arctic
Low Arctic
Boreal Forest

Table IV-1. Means and (standard deviations) of morphological characters in Meesia triquetra from three ecoclimatic regions and grand means and coeficients of variation for all specimens used in the morphometric analysis.

Character	Boreal Forest	Low Arctic	High Arctic	Grand Means	Coefficient of Variation
Growth increment length (mm)	9.95	8.49	7.27	8.6	53.7
	(3.9)	(5.36)	(3.31)	(4.6)	
Whorls per growth increment	10.17	9.18	6.78	8.7	42.9
	(4.20)	(2.99)	(1.93)	(3.7)	
Whorls per cm	10.62	12.77	10.78	11.4	36.7
	(3.75)	(4.32)	(3.38)	(4.2)	
Growth increment weight (mg)	0.68	0.68	0.58	0.7	59.9
	(0.39)	(0.37)	(0.25)	(0.3)	
Weight per mm growth (mg)	0.07	0.08	0.09	0.08	1081.7
	(0.02)	(0.02)	(0.03)	(0.04)	

Leaf length (mm)	2.07	2.03	1.91	2.01	22.5
	(3.41)	(4.71)	(2.87)	(4.52)	
Partial leaf length (mm)	1.49	1.47	1.35	1.44	24.4
	(2.52)	(36.0)	(2.18	(3.51)	
Leaf width (mm)	0.45	0.45	0.52	0.48	22.6
	(0.08)	(0.09)	(0.07)	(0.11)	
Leaf shape	3.40	3.19	2.67	3.1	27.8
	(0.59)	(0.78)	(0.57)	(0.8)	
Cell length (um)	32.40	34.34	33.88	30.9	40.2
	(7.35)	(9.15)	(7.42)	(12.4)	
Cell width (um)	12.74	13.27	13.99	12.5	32.0
	(2.12)	(2.52)	(2.01)	(4.0)	

Two leaves per stem were chosen randomly for leaf measurements. The following morphological characters were measured in micrometres with a Bioquant digitizer (after Vitt and Marsh, 1988): leaf length, leaf apex to the widest point of the leaf along the costa (partial length), and half leaf width at the widest point of the leaf (Fig. IV-2). Half leaf width was taken rather than the whole leaf width because the keeled leaves of M. triquetra do not lie flat on microscope slides. This character will be referred to as leaf width hereafter. Leaf shape was calculated by dividing leaf partial length by leaf width.

Cell length and cell width were measured in five cells on each of two leaves taken from each of the three stems examined per herbarium specimen. Five non-marginal cells, in a row perpendicular to the costa, were selected for measurement near the apex where the leaf is 15 to 20 cells wide.

Data Analysis

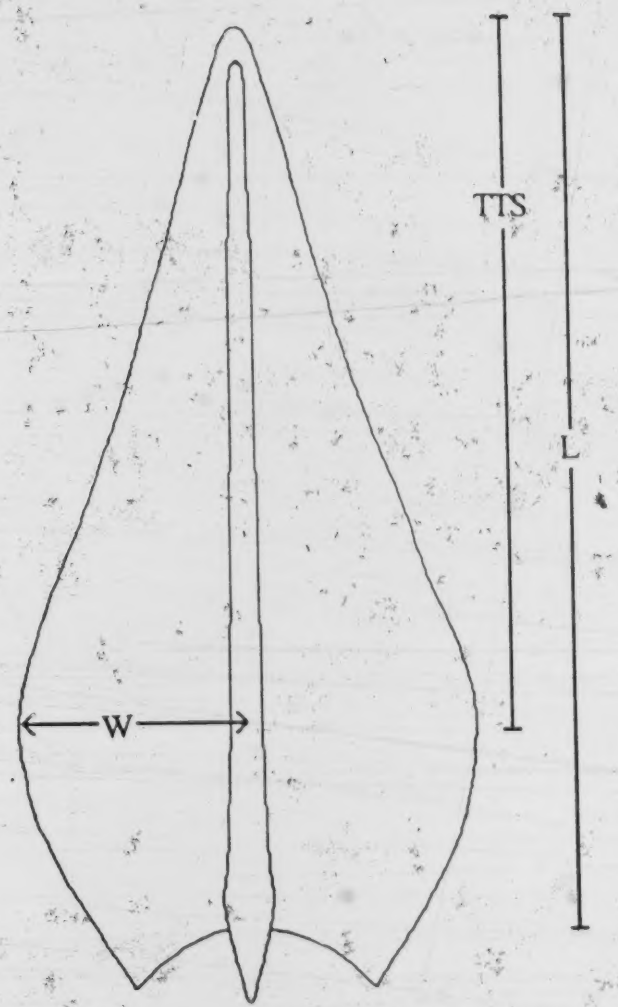
The distributions of all characters were tested for normality (SAS Institute Inc. 1982). Characters with non-random distributions were transformed either with a square root or natural logarithm transformation.

Four statistical analyses were performed on the data: regression analysis, principal components analysis, discriminant analysis, and an analysis of variance. I considered all four analyses necessary because of the complex and varied nature of the data. A single analysis may have produced spurious results, whereas the conclusions from several analyses can be compared to provide a more definitive interpretation.

Regression Analysis

The latitude of each of the 109 collection localities was converted from degrees and minutes to a single value. The degrees were represented in the first two or three digits,

Fig. IV-2. Leaf measurements used in the morphometric analysis of Meesia triquetra: length (L), width (W), and apex to widest point of the leaf along the costa (TTS).


TTS
L
W

The last two digits were a score of 00 to 99 representing the percent of the degrees measured by the minutes (i.e. 57° 30' would be converted to 5750).

Each of the 11 morphological characters was regressed against latitude to determine whether any of the characters vary significantly with latitude.

Principal Components Analysis

The means and variances of each character at each of the 109 collection sites were used as 22 separate variates in a principal components analysis (PCA). PCA was considered an appropriate ordination technique for this study because it assumes that the ordinated units vary linearly along the gradients in question (Minchin 1987). If morphological characters vary with latitude, I would expect them to vary linearly or nearly linearly because of the nature of the gradient. The results from the regression analysis support this assumption.

Site scores from the first two principal components were regressed separately against latitude to determine whether linear combinations of morphological characters vary significantly with latitude.

Multivariate Discriminant Analysis

A discriminant analysis (SAS Institute Inc. 1982) was performed to examine the morphological relationships of specimens classified on the basis of ecoclimatic regions. The three ecoclimatic regions used in this study were: Boreal, south of the treeline; Low Arctic, from tree line north to the coast of the continent; and High Arctic, all of the islands in the Arctic Archipelago (Fig. IV-1).

Multivariate Analysis of Variance

The University of Alberta analysis of variance computer program (UANOVA, Taerum 1989) was used to perform multivariate analyses of variance (MANOVAs) on the data

generated by the morphometric analysis. The data in this study were nested; cells within leaves, leaves within plants, plants within sites, and sites within ecoclimatic regions. A nested analysis of variance allows the researcher to determine first whether there is a significant difference among groups, and second, at what level of nesting the greatest amount of variation occurs. In a MANOVA the researcher can also determine which variables contribute the most to differences among groups. Three nested MANOVAs were performed to determine whether there were significant differences amoung groups and to determine the relative variance attributable to each measurement at the cell, leaf, and plant levels of nesting.

A multiple comparison, multivariate t-test was performed on the data at all three levels of replication with the Bonferroni procedure (Milliken and Johnson 1984) to determine the significant morphological differences among ecoclimatic regions.

Results

Morphometric analysis

The means, variances, and coefficients of variation of the 11 morphological characters measured are summarized in Table IV-1 (raw data are listed in Appendix 2). Leaf measurements have relatively low coefficients of variation in comparison to the plant and cell measurements. Weight per mm growth has the highest coefficient of variation at 1081.7 which is two orders of magnitude greater than coefficients of variation for any other character.

Regression Analysis

All of the measured morphological characters of Meesia triquetra vary significantly with latitude with the exceptions of the number of leaf whorls per cm and cell length (Table IV-2). However, very little of the morphological variance found in M. triquetra is accounted

Table IV-2. Regression of individual morphological characters and of principal component site scores of twenty-two morphological variates of Meesia triquetra against latitude.

Character	n	r^2	Significance
Growth increment length	327	0.099	***
Growth increment length	327	0.157	***
Whorls per growth increment	327	0.005	NS
Growth increment weight	326	0.019	*
Weight per mm growth	326	0.046	***
Leaf length	654	0.040	***
Partial leaf length	654	0.047	***
Leaf width	654	0.052	***
Leaf shape	654	0.160	***
Cell length	3270	0.001	NS
Cell width	3270	0.010	***
Principal component 1	109	0.086	**
Principal component 2	109	0.168	***

*, $p < 0.05$; **, $p < 0.005$; *** $p > 0.0001$

for by the latitudinal gradient. Character variation accounted for by latitude ranges from 0.99% in cell width to 16.04% in leaf shape. Growth increment length, number of leaves per growth increment, growth increment weight, leaf width, leaf length, and leaf partial length decreases with latitude, while weight per mm growth, leaf width, and cell width increases with latitude. Leaves appear to range from long and slender in the south to short and squat in the north (Fig. IV-3), although there is great variation around this trend.

Principal Components Analysis

Principal components analysis was based on the means and variances of the 11 morphological characters for each site. The site scores of both principal components 1 and 2 decrease significantly with latitude but, as in the regression analysis, the amount of variation in these scores accounted for by latitude is low: 8.6% and 16.8% respectively (Table IV-2). Furthermore, the two principal components only account for 35.3% of the variation in the data. Character loadings on the principal components are fairly even, rendering the components impossible to interpret.

Discriminant Analysis

This analysis discriminates among specimens of Meesia triquetra collected from different ecoclimatic regions using morphological data; 83% of High Arctic, 70% of Low Arctic, and 64% of Boreal Forest specimens are correctly classified (Table IV-3). Twenty-eight (26%) of the specimens are misclassified by the analysis and of those only 5% are not classified into adjacent regions (e.g. Boreal specimens classified as Arctic by the analysis).

Fig. IV-3. Meesia triquetra leaves from: A) Alberta 52° 42'N, Vitt 24198 (ALTA); B) British Columbia 52° 25'N, Jamieson 3091 (ALTA); C) Alaska 68° 07'N, Steere 650719-14 (ALTA); D) Northwest Territories 67° 47'N, Steere 10747 (NY); E) Northwest Territories 75° 40'N, Vitt 5465 (ALTA); F) Northwest Territories 74° 40'N, Schofield 209 (NY).

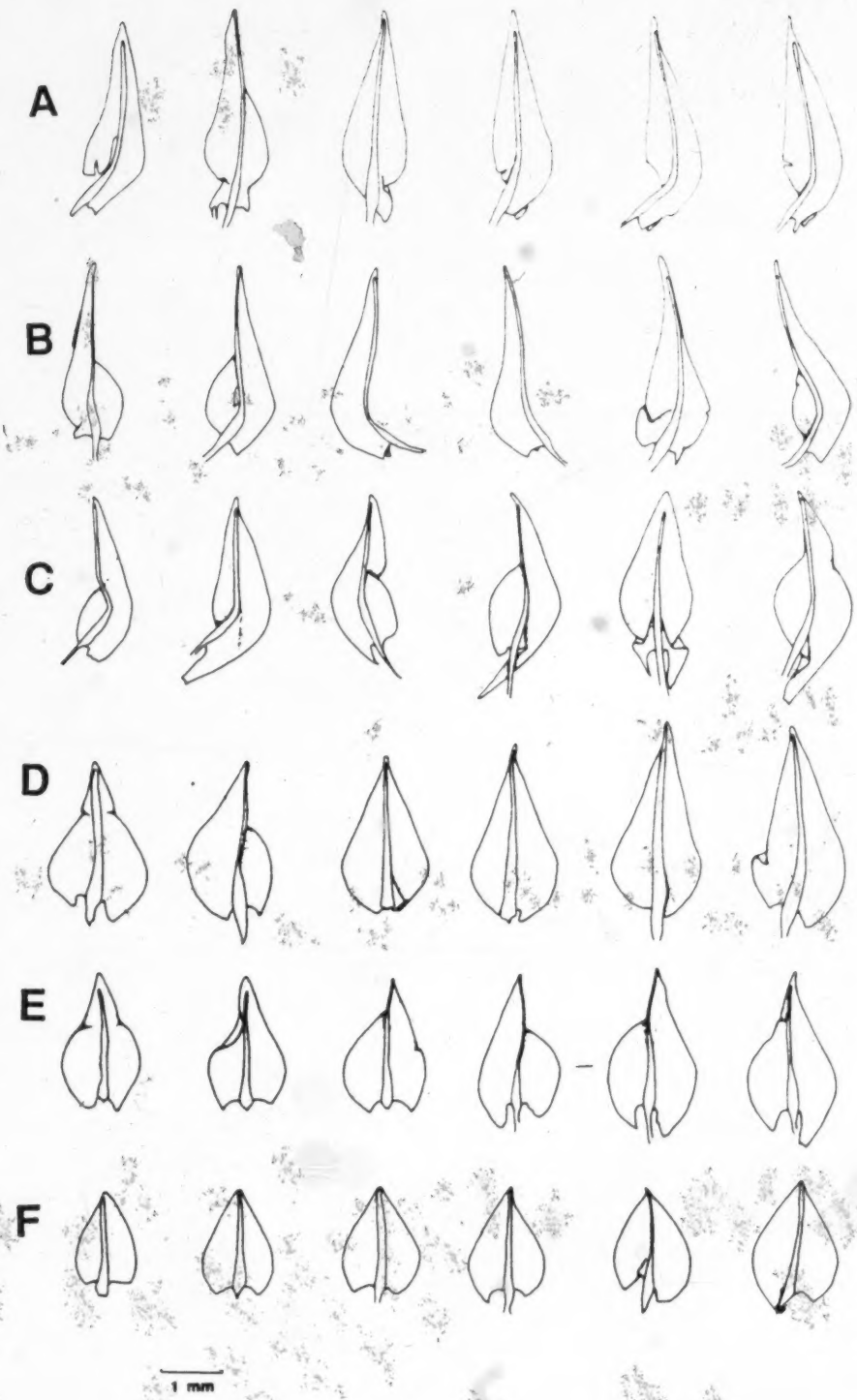

A
B
C
D
E
F
1 mm

Table IV-3. Ecoclimatic region classification of Meesia triquetra specimens by discriminant analysis of morphological characters. Numbers and (Percents)

		Into Ecoclimatic Region			
		High Arctic	**Low Arctic**	**Boreal Forest**	**Total**
From Eco-climatic Region	**High Arctic**	30 (83)	4 (11)	2 (6)	36 (33)
	Low Arctic	3 (8)	26 (70)	8 (22)	37 (34)
	Boreal Forest	4 (11)	7 (19)	25 (69)	36 (33)
	Total	37 (34)	37 (34)	35 (32)	

Multivariate Analysis of Variance

Plant Level

The MANOVA indicates significant differences in the morphology of Meesia triquetra among ecoclimatic regions at the plant level of replication (Table IV-4). Furthermore, the multiple comparison t-test indicates that all three ecoclimatic regions are significantly different from one another ($p < 0.017$). The characters that contribute most greatly to morphological differences among ecoclimatic regions, at the plant level of replication, are annual growth increment length, weight per mm of growth, leaf width, and leaf shape as indicated by high significance levels shown in Table IV-4.

There is also significant multivariate variation among sites at the plant level of replication (Table IV-4). All characters contribute significantly to differences among sites and vary more between sites than within sites with the exceptions of leaf width, leaf shape, cell length, and cell width (Table IV-5).

Leaf Level

At the leaf level of replication, the MANOVA indicates significant differences among ecoclimatic regions (Table IV-6). The multiple comparison t-test indicates that there is no significant morphological difference in specimens collected from the Low Arctic and Boreal ecoclimatic regions ($p = 0.05$), and that specimens collected from the High Arctic region are significantly different in their morphology from the other two regions ($p < 0.016$). These differences are mostly attributable to variation in leaf width and leaf shape as indicated by high significance levels in these characters shown in Table IV-6. All characters contribute to significant differences among sites, although leaf width, cell length, and cell width vary more within sites than they do among sites (Table IV-7). Significant differences among plants are attributable to leaf length, leaf partial length, leaf

Table IV-4. Summary of MANOVA results at plant level of replication. Significance of variation morphological characters.

Character	Ecoclimatic Region	Site
Multivariate	***	***
Growth increment length	*	***
Whorls per growth increment	***	***
Whorls per cm	NS	***
Growth increment weight	NS	***
Weight per mm growth	**	***
Leaf length	NS	***
Partial leaf length	NS	***
Leaf width	**	***
Leaf shape	***	***
Cell length	NS	***
Cell width	NS	***

*, $p < 0.05$; **, $p < 0.005$; *** $p > 0.0001$

Table IV-5. Summary of MANOVA results at plant level of replication. Morphological character variance between sites and between plants. Cell measurements 1 to 5 refer to five separately measured cells from each leaf in the morphometric analysis.

Character	Between Sites	Between Plants
Growth increment length	0.221	0.044
Whorls per growth increment	0.1	0.04
Whorls per cm	0.107	0.025
Growth increment weight	0.034	0.017
Weight per mm growth	0.002	0.001
Leaf length	26.505	8.617
Partial leaf length	11.958	7.341
Leaf width	2.377	2.537
Leaf shape	1.978	0.017
Cell length 1	0.045	0.059
Cell length 2	0.046	0.06
Cell length 3	0.045	0.062
Cell length 4	0.052	0.056
Cell length 5	0.042	0.063
Cell width 1	0.073	0.113
Cell width 2	0.079	0.126
Cell width 3	0.076	0.112
Cell width 4	0.067	0.148
Cell width 5	0.06	0.126

Table IV-6. Summary of MANOVA results at leaf level. Significance of variation in morphological characters.

Character	Ecoclimatic Region	Site	Plant
Multivariate	***	***	***
Leaf length	NS	***	***
Partial leaf length	NS	***	***
Leaf width	***	***	***
Leaf shape	***	***	***
Cell length	NS	***	***
Cell width	NS	***	NS

*, $p < 0.05$; **, $p < 0.005$; *** $p > 0.0001$

Table IV-7. Summary of MANOVA results at the leaf level of replication. Character variance between sites, between plants, and between leaves.

Character	Sites	Plants	Leaves
Leaf length	15.644	6.647	3.947
Partial leaf length	11.955	5.361	4.078
Leaf width	2.472	1.842	1.353
Leaf shape	0.033	0.009	0.18
Cell length 1	0.074	0.002	0.224
Cell length 2	0.078	0.004	0.224
Cell length 3	0.076	0.001	0.23
Cell length 4	0.068	0.028	0.243
Cell length 5	0.061	0.018	0.217
Cell width 1	0.045	0.006	0.107
Cell width 2	0.047	0.005	0.108
Cell width 3	0.045	0.012	0.1
Cell width 4	0.051	0.003	0.106
Cell width 5	0.042	0.019	0.088

width, and leaf shape. Cell width, cell length, and leaf shape vary more between leaves than between plants.

Cell Level

At the cell level of replication, there is a significant level of variation among ecoclimatic regions but it is only significant at the $p < 5\%$ level and this variation is due solely to cell width not cell length (Table IV-8). The results of the t-test at this level of replication are identical to those of the leaf level: the morphology of plants in the Low Arctic and Boreal ecoclimatic regions are indistinguishable ($p = 0.29$) and specimens in the High Arctic region are significantly different from those from the other two regions ($p < 0.017$). There are significant differences among both cell width and cell length which contribute to highly significant differences among sites, although both cell width and cell length vary more within sites than among sites (Table IV-9). Plants differ significantly from each other at the $p < 0.5\%$ level as a result of variation in cell length, although both cell width and cell length vary more within plants than between plants. Leaves vary significantly due to variation in both cell width and cell length, although both cell width and cell length vary more within leaves than they do between leaves.

Discussion

All four statistical analyses indicate that the morphology of Meesia triquetra varies over a Arctic-Boreal gradient. Although the variation along this gradient alone is not large, it is significant and subtantial such that discrimination among ecoclimatic regions along an latitudinal gradient is possible.

It is unlikely that the high coefficient of variation in the weight per mm growth character is actual, but rather an artifact. The weight of growth increments is very low (mean of 0.7 mg) and accuracy in measurement can be difficult to obtain. Weight per mm

Table IV-8. Summary of MANOVA results at cell level. Significance of variation in morphological characters.

Character	Ecoclimatic Region	Site	Plant	Leaves
Multivariate	*	***	**	***
Cell length	NS	***	**	***
Cell width	*	***	NS	***

*, $p < 0.05$; **, $p < 0.005$; *** $p > 0.0001$

Table IV-9. Summary of MANOVA reults at the cell level of replication. Character variance between sites, between plants, between leaves, and between cells.

Character	Sites	Plants	Leaves	Cells
Cell length	0.046	0.01	0.029	0.073
Cell width	0.07	0.009	0.055	0.178

growth is a composite character based on growth increment length and weight, thus the weight per mm growth compounds the variance from each of its composites. Despite the high degree of variation, this character is useful in comparing patterns of morphological variation in M. triquetra along a latitudinal gradient (as shown by the MANOVA).

Although all of the individual characters measured in this study exhibit a high degree of variation, there are trends of decreasing growth increment length, number of whorls per growth increment, growth increment weight, leaf shape, leaf partial length, leaf length, and trends of increasing weight per mm growth, leaf width, and cell width with increased latitude. Moreover, the PCA indicates that there are trends in linear combinations of morphological variables along this latitudinal gradient. All of these trends are significant, but they are not strong.

Generally these morphological trends parallel those of vascular plants; Meesia triquetra plants grow less in the North than in the South. Annual stem growth is decreased and fewer leaves are produced each year as latitude increases; furthermore, northern specimens tend to have shorter leaves. The vascular flora of the Arctic is well known to be relatively small in stature; this is controlled both genetically, through selective pressures such as wind abrasion, and phenotypically, due to limited resources and low temperatures (Bliss 1962; Chapin 1983; Savile 1972; and Warren Wilson 1966).

Leaf length decreases and leaf width increases with increasing latitude. Northern specimens possess leaves which are less acute than leaves from southern specimens. Microhabitat studies on the scale of individual stems are required to determine whether this morphological variation has adaptive significance, however, some inferences can be made based the literature. Because of the squarrose habit of M. triquetra leaves, stems with relatively wide leaves appear more compact than those with relatively slender leaves. Compact growth forms are characteristic of bryophytes in water stressed habitats (Birse 1957; and Gimingham and Birse 1957) and of the Arctic vascular plant flora in general

(Savile 1972). Perhaps the compact growth form of M. triquetra in the north is advantageous because it reduces temporal water loss and the risk of frost damage. Alternatively, the compact growth form may simply be a non-adaptive plastic response to the arctic environment; the arctic may be a sub-optimal habitat which limits the growth in M. triquetra.

The discriminant analysis indicates that the morphology of M. triquetra in each of the ecoclimatic regions is characteristic of that region. This is also born out in the MANOVA at the plant level of replication. Moreover, the multiple comparison t-tests indicate that the differences among ecoclimatic regions are greater between the High Arctic region and the Boreal and Low Arctic regions than between the Boreal and the Low Arctic regions at the leaf and cell levels of replication. Evidently temperate climates and possibly the presence of surounding forests have a effect on the morphology of M. triquetra. Forests surrounding fens in which M. triquetra grows will supply an influx of nutrients, provide protection against wind and its associated effects, and provide shade at certain times of the day.

The MANOVA has provided information to justify the morphometric analysis. Since there are highly significant differences between sites at all levels of replication and most characters vary more between sites than within sites, it can be concluded that sufficient measurements were taken per specimen to conduct the analyses. Characters which are most useful in determining patterns of variation in M. triquetra are the length of the growth increment, leaf length, leaf width, leaf shape, partial leaf length, and cell width, even though some of these characters vary more within sites than among sites. The number of leaves per cm and cell length appear to vary greatly within sites, thus are not considered useful characters for morphometric analysis in this moss.

In conclusion, Meesia triquetra varies in its morphology both along a latitudinal gradient and among ecoclimatic regions along an arctic-boreal gradient. The morphological

variation accounted for by this gradient is low but significant in all of the conducted analyses. A high degree of morphological variation was detected throughout the range of M. triquetra which was not accounted for by the arctic-boreal gradient. This variation may be due to genetic differences or the result of plastic responses to different microclimates among collection localities. Morphological variation due to either genetic variation or phenotypic plasticity may be used as an indicator of evolutionary flexibilty and of the potential for a species to evolve (Longton 1974). The morphology of M. triquetra varies significantly along at least one gradient indicating that this bryophyte has an active evolutionary potential.

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V. Growth of arctic and boreal populations of the brown moss Meesia triquetra under controlled conditions. [1]

Introduction

For decades bryologists have debated whether mosses have been arrested at a primitive stage in their evolution or whether they possess high evolutionary potential . Traditionally, views have paralleled those of Steere (1958) who wrote "Bryophytes are an ancient phylogenetic line or series of lines that have come to a dead end, evolutionarily speaking." He also stated that mosses are characteristic of primitive plant forms in that they lack a cuticle and exhibit clonal growth. Since most mosses have a dominant haploid stage, slightly deleterious mutations are strongly selected against, because they are never masked in the heterozygotic state. Also bryophytes are expected to demonstrate a high degree of inbreeding through monoecy which would also reduce genetic variability (Longton 1979a). Evolution of arctic bryophytes is thought to be particularly slow because sexual reproduction in mosses is even more reduced at high latitudes (Kallio and Saarnio 1986; and Savile 1972). Longton (1988) suggested that bryophytes are more dependent on phenotypic plasticity for variation than genetic adaptation.

Contrary to these ideas, other bryologists have found that mosses may possess a high potential to evolve. For instance Wyatt et al. (1989) have found extraordinarily high degrees of electrophoretically detectable genetic variation in Plagiomnium ciliare (C. Mull.) Kop., and I have found similar results in Meesia triquetra (Richt.) Aongstr. (chapter VI). Also, Brassard (1974) suggested that some arctic bryophytes may have evolved within the last 23,000 years. All variation, whether due to phenotypic plasticity or genetic differentiation, allows species to expand their distributions thereby exposing plants to new selective pressures. These selective pressures can lead to further variation and sometimes

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1. A version of this chapter has been submitted for publication. Montagnes. 1991. Canadian Journal of Botany.

speciation (Stearns 1989). Moreover, phenotypic plasticity is a genetically controlled trait (Bradshaw 1965; MacDonald et al. 1988; Schlichting 1986; and Stearns 1989) and bryophytes have been shown to be highly phenotypically plastic (Longton 1974).

Several authors have examined variation in bryophytes. Longton (1972, 1979a) found that Polytrichum alpestre Hopp. decreased in annual growth increment length and weight, leaf length, and number of leaves produced per year with latitude. Sphagnum species have a higher production rate in shaded areas than in open areas at Barrow, Alaska (Murray et al. 1989). Wehr and Whitton (1986) found that Rhynchostegium riparioides (Hedw.) Card. varied in robustness, leaf shape, and length, and in degree of leaf denticulation from springs and calcareous head-waters to large rivers with high sodium, ammonium, and phosphate concentrations. Busby et al. (1978) found that growth in Hylocomium spendens (Hedw.) B.S.G. was controlled by overstory vegetation and that Tomenthypnum nitens (Hedw.) Loeske growth was controlled by precipitation. Pohlia wahlenbergii (Web. et Mohr.) Andrews was found to be more productive along stream banks than on hill sides (Clarke et al. 1971). Hylocomium splendens shows great morphological diversity from a gigantic west coast form to a tundra form which lacks the characteristic stair-step fronds. Growth in this moss is controlled by environmental factors such as precipitation and continentality (Vitt 1989).

Although many authors have examined variation in bryophytes, few have followed through in their studies with common garden experiments or reciprocal transplants to determine whether the variation is a result of genetic differentiation or phenotypic plasticity. Only these sorts of experiments can be used to interpret variation. For instance, in greenhouse experiments, Birse (1957) found that moss growth forms were environmentally induced, not genetically controlled. Longton (1974) found that populations of Polytrichum strictum Menz. ex Brid. taken from a range of environments along a latitudinal gradient lost morphological differences when grown in a common

garden. Similar results were obtained with Bryum argenteum Hedw. (Longton 1981). He also found that antarctic populations of Polytrichum alpestre could maintain a positive net carbon gain in temperatures too low for boreal populations, which indicates ecotypic differences between the two populations.

Meesia triquetra is a rich fen indicator species of high fidelity occurring in North America from northernmost Ellesmere Island south to California and Montana in the west and Pennsylvania and Wisconsin in the east, and from western Alaska east to Newfoundland (Montagnes 1990). Vitt and Pakarinen (1977) were able to use the well developed annual growth increment markers in M. triquetra to estimate annual production of the bryophyte layer in sedge meadows at Truelove Lowland, Devon Island in the Canadian High Arctic. This moss is subject to a wide variety of environmental conditions over its extensive range. Annual growth increment weights and lengths in M. triquetra decrease with increasing latitude (chapter IV). Low temperatures, low nutrient availability, low light intensity, and the short growing season are considered the major factors controlling vascular plant growth in the arctic (Billings 1987; Bliss 1962; Chapin 1983; Savile 1972; Weilgolaski 1980; and Warren Wilson 1966). Severe arctic conditions, however, may pose more of an obstacle to vascular plants than bryophytes (Brassard 1974) as is shown by the dominance of mosses in many high latitude habitats and the fact that bryophyte annual productivity is much less reduced with increasing latitude than annual productivity in vascular plants (Vitt and Pakerinen 1977; and Weilgolaski 1980). The objective of this study was to determine whether variation in annual growth increment length of M. triquetra is genetically controlled or a result of phenotypic responses to different environments. Genetic differences among populations imply local adaptation or genetic drift, either of which are indicators of a potential to evolve.

Methods

In late July and early August of 1989 collections of live plants in their peat substrate to a depth of seven cm were made from one boreal and one high arctic fen. Specimens were placed in plastic bags and kept cool until their use in the fall.

The boreal fen is located along a pond margin near Edson, Alberta 5 km south on the west side of Highway 47 (55° 35' N, 116° 26' W) (Plate III-1). The site is located in a wooded area of the Alberta Plain at the eastern edge of the Rocky Mountain foothills and is underlain by Tertiary sandstones and shales, covered by hummocky ground moraine deposited by the Cordillerian glacier during the Wisconsinan period. The till is stoney, with limestone blocks (Clayton et al. 1977a). Elevations rise between 1200 and 1800 m above sea level (Drinkwater et al. 1969). This area is also part of a sand dune complex formed by glacial Lake Edson (Slack et al. 1980).

The climate of the Edson-Nordegg area is temperate with a July mean monthly temperature of 14.4°C. It has a frost free period (number of days between the last frost in the spring and the first frost in the fall) of approximately 80 days and recieves an average annual precipitation of 533 mm, with 305 mm falling during the frost free period (Alberta Environment 1988; and Drinkwater et al. 1969).

The area is dominated with Picea glauca (Moench) Voss, P. mariana (Mill) BSP., and Pinus contorta Loudon associations and is studded with occasional Populus tremuloides Michx. stands (Clayton 1977a; Drinkwater et al. 1969; Slack et al. 1980). There are abundant ponds and open mires in low lying areas among tree-covered hills.

The high arctic site is located in an extensive fen at Princess Marie Bay on Ellesmere Island, N.W.T. (79° 29' N, 75° 47' W) Canada Plate III-3. The fen is 6 km from the coast in an estuary lowland which extends north 20 km and is 5 km wide. The lowland is banked on either side by folded mountains of sedimentary limestone and sandstone laid down in the Ordovician and Silurian periods. The area was glaciated during

the Pleistocene and experienced postglacial marine submergence. Isostatic uplift is still occurring (Williams et al. 1980). Soils in this area are regosols of humid, loamy glacial till or fluvial deposits and are more poorly developed than those of the Edson area (Clayton et al.1977b).

Climate studies of the Princess Marie Bay area are few. The limited records show mean monthly July temperatures of 6.6°C, a frost free period of 37 days (Williams et al. 1980) and the total precipitation for the months of July and August of 26.1 mm (G. Henry unpubl. data). The Princess Marie Bay lowland is considered a polar desert . In general, the Princess Marie Bay area is cooler and dryer than the Edson area.

The vegetation of Princess Marie Bay is controlled for the most part by soil moisture. The land ranges from barren, or near barren, clay badlands, exposed rock and scree occasionally colonized by Dryas integrifolia M. Vahl, Saxifraga oppositifolia L., and Salix arctica Pall., to slightly more vegetated stable terraces which have, in addition to the above species, species of Carex, Lesquerella, and Braya. Species richness and vegetative cover is highest along seepage slopes and in wet sedge meadows (Williams et al. 1980).

Forty litres of water were collected from the high arctic and the boreal sites in acid washed plastic carboys. In addition to the carboys, two 250 ml polystyrene bottles and one 250 ml nalgene bottle were filled at each fen. Samples were kept in cool storage between collection and analysis. Fifteen water quality variables were measured in the surface water collected from each fen. Total phosphorus and dissolved phosphorus concentrations were measured on a Mitton Roy spectrophotometer after acid digestion. Ammonium and nitrate concentrations were measured on a Technicon autoanalyser II. Concentrations of sodium, potassium, calcium, and magnesium were determined through atomic absorption spectrometry. Sulphate and chloride concentrations were measured with a Dionex chromatograph. pH was measured in the field with a portable Extech pH meter.

Alkalinity was measured in the laboratory, as were water colour, turbidity and conductivity after the methods of Bierhuizen and Prepas (1985).

In the laboratory, the length of the penultimate annual growth increment in thirty stems from each population was measured with calipers to the nearest tenth of a mm. A t-test was performed to determine whether the length of the annual growth increments differed significantly between populations in natural conditions.

Ten, individual, unbranched, sterile Meesia triquetra stems were placed between 10 cm long velcro strips such that only 5 mm of growth emerged from the top edge of the strip. Thirty two replicates of 10 plants each were made from each of the two populations (640 stems in total). These replicates were grown in 200 ml of water in acid washed plastic tubs that were 6 cm deep and 12 cm in diameter. Half of the replicates from each population were grown in water from the high arctic fen and half of the replicates were grown in water from the boreal fen. Also half of the replicates were fertilized with ammonium nitrate as to raise the nitrogen content to 1 $mg \cdot L^{-1}$ ammonium and 6 $mg \cdot L^{-1}$ nitrate. Thus, a fully factorial design was achieved with two M. triquetra populations, two types of water, and two levels of fertilization.

Treatments were randomly placed in the growth chamber and the tubs were rotated every week to reduce any uncontrolled effects due to temperature or lighting gradients in the chamber. The tubs were set in a 4 cm deep water bath to ameliorate temperature differences due to lighting on the growth bench. The lighting was held constant with 16 hours of light at an intensity of 300 μ mol s^{-1} m^{-2} per 24 hour period. The water bath had daily maximums of 18°C and daily minimum temperatures of 10°C. Relative humidity was held at 65%. Both photoperiod and temperatures more closely resembled the boreal growing season than the high arctic growing season. Every day the water levels in the tubs were restored to 200 ml with distilled, de-ionized water. The plants were grown for seven weeks. At the fourth week the water was changed and the fertilized treatments were

re-fertilized. At the end of the growing period the amount of growth in each stem, beyond the original 5 mm, was recorded as mm of primary stem elongation. Also the number and length of any branches arising from the 5 mm growth were recorded. Branches arising from below the point where the stem emerged from the velcro were ignored. The total growth of primary stem elongation and secondary branches arising from the original 5 mm of stem was recorded in mm as secondary stem elongation. Dry weights were not taken because small lengths of Meesia triquetra (< 3 mm) weigh very little and the inaccuracy in measurement was considered too high for a reasonable analysis. Two partially nested analyses of variance (ANOVAs) were performed on the data (model: population + water treatment + nitrogen treatment + population x water treatment + population x nitrogen treatment + water treatment x nitrogen treatment + replications (population, water treatment, nitrogen treatment) + residual). The first used the primary stem elongation data only and the second used the secondary stem elongation data.

Results

Nitrate levels are much higher in the high arctic than the boreal water, whereas ammonium levels are higher in the boreal water (Table V-1). Both total phosphorus and total dissolved phosphorus concentrations are higher in the boreal water than the high arctic water, as are sodium, potassium, calcium, and magnesium concentrations. Conductivities are 305 microsiemens in the high arctic water and 350 microsiemens in the boreal water. The pH is 8.1 in the high arctic water and 7.6 in the boreal water, while alkalinity is slightly higher in the high arctic water.

The average annual growth increment length for the high arctic population is 7.6 +/- 2.8 mm and that of the boreal population was 8.6 +/- 3.3 mm. There is no significant difference in annual growth increment length between the two populations ($p = 0.18$). I found that the average annual growth increment length from 36 high arctic and 36 boreal

Table V-1. Water quality variables of surface water from a high arctic and a boreal fen in which Meesia triquetra occurs.

Variable	High arctic site	Boreal site
Total phosphorus ($\mu g \cdot L^{-1}$)	1.3	32.8
Total dissolved phosphorus ($\mu g \cdot L^{-1}$)	1.6	8.8
NO_3-N ($\mu g \cdot l^{-1}$)	6.8	0.0
NH_4-N ($\mu g \cdot l^{-1}$)	3.1	4.8
Na ($mg \cdot l^{-1}$)	0.3	1.5
K ($mg\ l^{-1}$)	0.1	0.9
Ca ($mg \cdot l^{-1}$)	37.4	40.2
Mg ($mg \cdot l^{-1}$)	6.4	7.6
SO4 ($mg \cdot l^{-1}$)	2.4	0.0
Cl ($mg \cdot l^{-1}$)	0.9	3.3
pH	8.1	7.6
Alkalinity $meq \cdot l^{-1}$	154.2	173.9
Conductivity (microsiemens)	305	350
Turbidity (nephlometric turbidity units)	7.5	60.0
Colour ($mg\ Pt \cdot l^{-1}$)	0.9	10.0

Meesia triquetra populations were 7.3 +/- 3.3 mm and 9.9 +/- 3.9 mm respectively (chapter IV). The populations used in this experiment possess annual growth increments lengths which fall within the ranges of other populations found in their respective ecoclimatic regions. Although there is a significant trend of decreasing annual growth increment length with latitude (chapter IV), the average annual growth increment lengths of stems from the two ends of the latitudinal gradient are not significantly different.

None of the growth data in any of the treatments is distributed normally, in fact the majority is bimodally distributed, with a large number of stems having no growth at all. The high arctic population has 134 zero growth data points of 320 plants, and the boreal population has 59 zero growth data points, of 320 plants, in the primary stem elongation data set; whereas, the high arctic population has 126 zero growth data points and the boreal population has 29 zero growth data points in the secondary stem elongation data set (Appendix 3). Fewer stems of each population have zero growth points in the secondary stem elongation data set because many stems that did not elongate produced new branches. Stems which exhibited growth fell into fairly normal distributions. This led to some difficulty in analysis. Zero growth data points were not excluded from analyses incase they were real values caused in some way by the treatment or characteristic of the populations. If the zero growth data points are left in the analysis the assumption of normal distribution is violated, and no appropriate nonparametric test is available for such data. It was decided to perform ANOVAs on the data with and without the zero growth data points and to compare the results. The probabilities of significance were extremely high in most cases and the results were similar between ANOVAs with and without zero growth data points so I believe that the ANOVA was suitably robust to handle the data, however the conclusions made in this study should be regarded with the statistical violations in mind.

All four analyses (of primary stem elongation, secondary stem elongation, and with and without the zero growth data points included in the analysis) indicate highly significant ($p << 0.005$) differences in growth between the high arctic and the boreal populations, with the plants from the high arctic population growing much less than those from the boreal population (Fig. V-1-A and Table V-2). Neither effects from the nitrogen treatment, the different waters, nor any interaction effects are significant at the $p < 0.05$ level (Fig. V-1-B and V-1-C) except for the interaction effect of population and nitrogen treatment in the ANOVA of secondary stem elongation data which includes the zero growth data points. The probability of significance of this interaction is quite low ($p = 0.0493$), relative to the differences in growth between populations, and is not supported by any of the other analyses so the effect is not considered biologically significant.

Discussion

Meesia triquetra shows no plastic response to the aquatic environment in which it grows; stems from either the high arctic or boreal populations grow the same amount in boreal water as they do in high arctic water, despite the fact that the boreal water contains less nitrogen, and more sodium, potassium, calcium, magnesium, and phosphorus than the high arctic water. Also the pH of the boreal water is close to the mean pH for fens in which M. triquetra occurs, whereas the high arctic water has a pH at the extreme upper limit of the moss (Montagnes 1990).

The nitrogen fertilization treatment had no significant effect on the growth of Meesia triquetra. At similar levels of nitrogen fertilization, Austin and Weider (1987) found that growth in Sphagnum pulchrum (Lindb.) Warnst. was diminished, but that growth in S. fallax Klinggr. and S. henryense Warnst. was enhanced. Rudolf and Voigt (1986) found that growth in S. magellanicum Brid. increased with fertilization treatments of nitrate much higher than was used in this study, but growth decreased with similarly

Fig. V-1. Results of growth experiment under controlled conditions. Effects of factors are averaged over treatments. V-1-A means of growth data from high arctic and boreal populations of Meesia triquetra, V-1-B means of growth in plants grown with and without nitrogen fertilization, V-1-C means of growth in plants grown in water taken from an arctic fen and water taken from a boreal fen, from four data sets: 1) primary stem growth with zero growth data points included, 2) primary stem growth with zero growth points excluded, 3) secondary stem growth with zero growth points included, 4) secondary stem growth with zero growth points excluded. Error bars represent standard deviation of the mean.

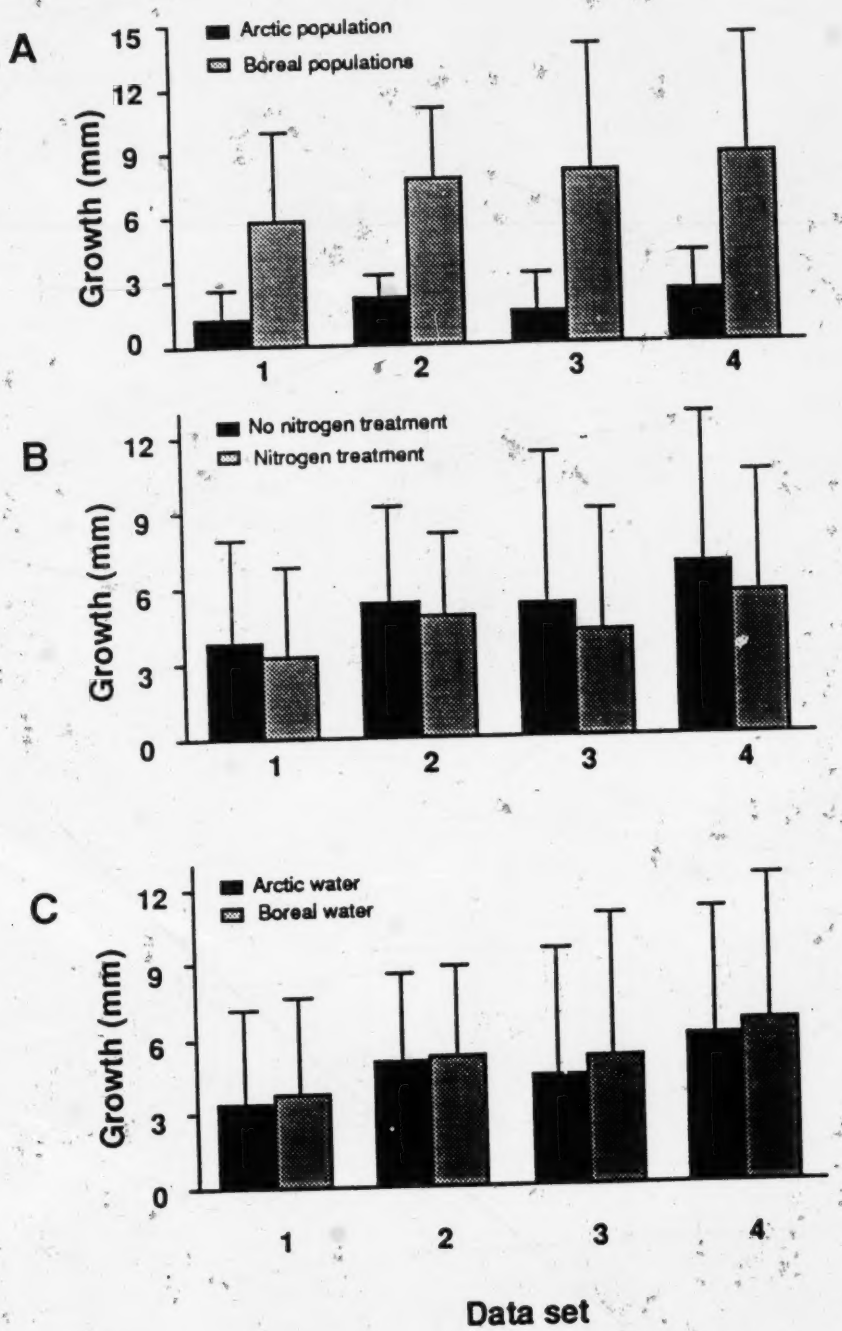
A
Arctic population
Boreal populations
Growth (mm)
15
12
9
6
3
0
1
2
3
4
B
No nitrogen treatment
Nitrogen treatment
Growth (mm)
12
9
6
3
0
1
2
3
4
C
Arctic water
Boreal water
Growth (mm)
12
9
6
3
0
1
2
3
4
Data set

Table V-2. Results of Meesia triquetra growth experient. Probability of significance values of treatment and interaction effects for analyses of variance of four data sets: 1) primary stem growth with zero growth data points included, 2) primary stem growth with zero growth points excluded, 3) secondary stem growth with zero growth points included, 4) secondary stem growth with zero growth points excluded. A * represents interaction.

	Data Set			
Effect	1	2	3	4
Population	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Water	0.2793	0.3380	0.1591	0.2663
Nitrogen	0.0872	0.1199	0.0606	0.1170
Population*Water	0.4113	0.3219	0.2477	0.4120
Population*Nitrogen	0.0920	0.0767	0.0493	0.1157
Water*Nitrogen	0.5501	0.7460	0.7318	0.9110

high levels of ammonium. Press et al. (1986) found decreased growth in S. cuspidatum with very low levels of nitrogen fertilization (0.01 mM NO_3NH_4). Evidently the reaction of moss species to increased nitrogen is species specific and depends on the type of nitrogen which is increased in the system; however, it appears that added nitrogen levels must be higher than those used in this study to induce a growth response in M. triquetra.

In the experiment , almost 100 more high arctic plants exhibited zero growth than boreal plants. Although it is impossible to discern whether the stems which did not grow were dead or whether they were in a dormant phase, mosses are generally considered to have opportunistic growth (Longton 1980), thus the stems were most likely dead. Under the experimental conditions the boreal population had a higher survival rate than the high arctic population. Any difference in hardiness between the two populations at the begining of the experiment was not due to previous nutrient limitation in the high arctic. Neither the nitrogen fertilization nor the boreal water enhanced the growth of the high arctic plants, thus they were not limited by low nutrient availability in the northern fen. The difference in survival between the two populations may be due to environmental effects, as the experiment was held in a boreal type environment which may have been stressful to the high arctic plants.

Under natural conditions there is no significant difference in growth between the high arctic and boreal populations, however under the experimental conditions the difference is significant with the high arctic plants growing far less than the boreal plants. Since the experimental conditions simulated a boreal growing season rather than a high arctic growing season, decreased stem elongation in the high arctic plants must be due to their inability to metabolise efficiently under boreal conditions. The high arctic population has adapted either genetically or plastically to the high arctic environment and may be unable to assume its normal growth pattern in shorter photoperiods or warmer temperatures than are normally experienced in the high arctic. Kallio and Saarnio (1986)

performed reciprocal transplant studies along a latitudinal gradient on Pleurozium shreberi (Brid.) Mitt., Hylocomium splendens, and Racomitrium lanuginosum (Hedw.) Brid. and found that photosynthesis increased in the plants which were moved south. They also found that this change in photosynthesis was not in fact a genetic differentiation between the high arctic and boreal plants, but a plastic response to light levels; after two years the photosynthetic apparatus had changed and the photosynthetic rates decreased to normal ranges for boreal plants. Decreased growth in high arctic Meesia triquetra plants in boreal conditions may be a plastic response to a change in environments rather than a genetic difference between the high arctic and boreal populations. The high arctic plants may be able to resume growth comparable to boreal plants after a period of adjustment to boreal conditions. Alternatively, the difference may indeed be a result of genetic differentiation between the populations.

Whether the differences in growth response are genetic or plastic, Meesia triquetra shows the ability to adapt physiologically to different environments. Local adaptation through genetic differentiation or phenotypic plasticity can enable species distributions to expand, thereby exposing the plants to new selective pressures. The new selective pressures may, in turn, lead to further differentiation among populations or even speciation (Stearns 1989). Meesia triquetra shows extensive differentiation in terms of growth response to environmental conditions, thus demonstrates a relatively high potential to evolve. Although M. triquetra has a very limited chemical ecology (Montagnes 1990), it is apparently unrestricted in its distribution by other environmental factors such as temperature and light because of its ability to adapt to local conditions.

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VI. Isozyme variation in the brown moss, Meesia triquetra, along an arctic-boreal gradient. [1]

Introduction

Throughout the last decade bryologists have debated the rate of evolution in mosses and liverworts. Traditional views regard bryophytes as evolutionarily unspecialized in comparison to tracheophytes, as they are phylogenetically older than these plant groups but are far less differentiated (Crum 1972; and Szweykowski 1984). Differentiation of the three major taxonomic divisions within the bryophytes (mosses, liverworts, and hornworts) was completed by the Permian period (Anderson 1980; and Ennos 1990), and modern moss genera and species were present by the Cenozoic (Vitt 1984). Morphological similarities among congeners are used as evidence of slow evolution (e.g. Daniels 1982). In fact, Crum (1966) has gone as far to say that evolution at the specific level appears to be at a standstill.

Five lines of evidence support the view that bryophytes have a slow evolutionary rate. First, some taxonomic groups are morphologically uniform with very few varieties or endemics and a small number of species per genus, which, according to Crum (1972), indicates a depleted biotype and a genetic poverty associated with the old age of the phylum. Also, the fossil record indicates that bryophytes diversified into the major taxonomic divisions of mosses, liverworts, and hornworts by the Permian period and that very few major morphological changes have occurred since (Anderson 1963; Crum 1972; Cummins and Wyatt 1981; Dewey 1989; Krzakowa and Szweykowski 1979; and Wyatt et al. 1989). However, several bryologists have suggested that the fossil record is far too scant to be used as conclusive evidence in the debate on the rate of evolution in bryophytes (Khanna 1964; Krassilov and Schuster 1984; and Miller 1984).

- 1. A version of this chapter has been submitted for publication. Montagnes, Bayer and Vitt 1991. Heredity.

Second, some bryophyte species occur as disjunct populations as far apart as the two poles. Tracheophytes, with similar distributions, have undergone speciation so that they are related to each other at the generic or familial rank, while disjunct populations of bryophytes are often of the same species. Such disjuncts can be viewed as relict populations that have perhaps not undergone adaptive radiation or even random genetic drift to render disjunct populations taxonomically different from the rest of the species (Anderson 1963; Crum 1966; Cummins and Wyatt 1981; Dewey 1989; Krzakowa and Szweykowski 1979; and Szweykowski 1984). In some bryophyte species, the disjunct populations have become asexual which further reduces their chances for evolutionary changes (Longton 1976). Disjunct populations may have established relatively recently through long range dispersal, however the populations reflect tectonic events as do disjunct populations of vascular plants; moreover, current understanding of bryophyte distributions indicates that long range dispersal is far less important than slow step by step dispersal across wide areas (van Zanten and Pocs 1981; and Wyatt et al. 1989a).

Third, many bryologists believe that the slow rate of evolution in mosses and liverworts is chiefly due to the dominant haplophase in the bryophyte life cycle. Diploids have the evolutionary advantages of increased genetic variation due to heterozygosity, the ability to aquire mutations twice as fast, and the ability to mask deleterious recessive alleles (Innes 1990). Haploid organisms, on the other hand, are believed to have low gene diversity because a slightly deleterious mutation will be strongly selected against in the gametophyte stage, and since mutations that are deleterious in one environment may be advantageous in another, the chances of adapting to new environments through mutation alone are reduced (Crum 1972; Cummins and Wyatt 1981; Daniels 1982; Innes 1990; Krzakowa and Sweykowski 1979; Longton 1976; Sweykowski 1984; and Yamazaki 1981). It is difficult to test this theory in slow growing organisms, however, Paquin and

Adams (1983) found that diploid yeast evolved 1.6 times faster than haploid yeast. Although mutations are more often deleterious, an advantageous mutation in a haploid organism would be selected for strongly, and any mutation that was not selected against may reproduce rapidly in mosses through vegetative reproduction (Anderson 1963).

Fourth, because of their small stature and relatively restricted niche range, bryophyte species are thought to be subjected to very few new selective pressures (Crum 1966; Cummins and Wyatt 1981; Dewey 1989; and Longton 1976). Mosses can avoid macro-environmental change because they are well suited to specific micro-environments, thus they avoid the pressures that are exerted on larger plants though geologic time (Anderson 1963; and Crum 1972) or presumeably over large environmental gradients as changes in latitude. Supposedly because bryophytes are not subjected to new selective pressures, they do not undergo adaptation, hence they appear to have a low evolutionary potential.

Finally, bryophytes have a particularly short gene flow distance which is thought to increase inbreeding, reduce sexual recombination, and reduce the rate of evolution (Anderson 1980; Cummins and Wyatt 1981; and Wyatt et al. 1989b). Sperm require a continuous film of water from antheridium to archegonium to achieve fertilization. This provides a formidable reproductive barrier to monoicous species and even more of a barrier to dioicous or phyllodioicous species which are, by definition, obligate outcrossers (Khanna 1964). Some moss species increase the distance sperm can travel by producing antheridia in splash cups, but even this mechanism increases gene flow to only a maximum of approximately 15 cm (Wyatt 1982). Potentially, spores can waft into the upper atmosphere and be carried for 19,200 kilometers or more (Longton 1976). Although long range dispersal may be hindered by the size of some spores (larger than 25 μm), spores may be transported long distances by animal vectors (van Zanten and Pocs 1981). According to several bryologists, there is a trend towards monoicy and even abandonment

of sexual reproduction in mosses, presumably because of the costs associated with long distance sperm travel (Cummins and Wyatt 1981; Dewey 1989; and Khanna 1964), thus species can become almost genetically identical throughout their range (Anderson 1963).

Fragmentation can become an important mode of reproduction and gene dispersal as almost every part of the moss plant, except the antheridia, can regenerate (Anderson 1980). Fragmentation and vegetative reproduction are particularly important in polar regions where sporophyte production is much lower than in temperate or tropical regions (Crum 1972; Holmen 1960; Longton 1976; Schofield 1985; and Smith 1987). Inbreeding and vegetative reproduction lead to reduced gene diversity which in turn reduces the evolutionary flexibility of a species; prior gene diversity is required before temporal, spatial, or ecological reproductive isolating mechanisms can affect evolutionary rates (Ennos 1990; Farris 1988; and MacNaire 1989). Therefore, we can expect that gene diversity will be reduced in arctic mosses relative to mosses of lower latitudes, and possibly that populations of mosses in the north will have lower genetic diversities relative to their conspecifics in the south.

These five lines of evidence have led bryologists to believe that evolution is slow in the bryophytes. Crum (1972) went as far as to say that mosses are "evolutionary failures" and that "for ecological success they have paid in genetic uniformity and slow speciation", however, all of the above hypotheses are based on inference and not on empeirical data. Evolution is based on changes in gene frequencies and so it is at gene frequency that we should look for information on the rate of evolution in bryophytes (Krzakowa and Szweykowski 1979; and Wyatt 1982).

Several electrophoretic studies indicate that the level of gene diversity in bryophytes is much higher than expected and is in some species comparable to gene diversity in angiosperms. For instance, the liverwort Conocephalum conicum (L.) Dum. has a genetic variability comparable to most diploid species. Seven of 11 enzyme systems

examined in this liverwort were found to vary in their electrophoretic phenotypes at two levels (Yamazaki 1981). At the world level, there are two isolated forms which were later discovered to have different morphology, growth rates, and produced different phenolic compounds. Over 1000 specimens were examined and no indication of recombination between the two types was found (Sweykowski 1982). The second level of variation is at the local level where diversity was higher than at the world level because of many rare alleles (Sweykowski 1984).

Electrophoresis has been used in taxonomic investigations of the genus Pellia. Krzakowa (1981) found P. endiviifolia Dum. and P. epiphyllia (L.) Corda to be distinct species and that many other Pellia species were synonomous with one or the other taxon, while Zielinski (1987) found that populations of P. endiviifolia in Poland and Japan were as genetically different as many angiosperm species. He also found that P. neesiana (Gottsche) Limpr. and P. borealis Lorb. have genetic diversities much lower than most angiosperm species (H_t = 0.025 and 0.045 respectively). Possibly the discrepancy in these studies resulted because Krzakowa used only peroxidase to indicate differences among species, whereas Zielinski used 10 different enzymes. Peroxidase and esterase are nonspecific enzymes which often produce many isozymes leaving these systems difficult to interpret; also the activities of these enzymes are known to be affected by environmental conditions (Wyatt et al. 1989a). If peroxidase or esterase markers are used in determining genetic variability they should not be used alone, but with more reliable systems. Much of the work done on gene diversity in bryophytes has utilized these non-specific enzymes. In another example, Krzakowa and Szweykowski (1979) used three peroxidase loci to examine variation in Plagiochilla asplenioides (L.) Dum. They found substantial differences between two geetic races within Poland and a high level of variation within colonies located within populations.

Szweykowski and Zielinski (1983) found four genotypes of Plagiothecium undulatum (Hedw.) B.S.G. in Poland, and that individual colonies of this moss were electrophoretically monomorphic. Shaw et al. (1987) found genetic differences between Climacium americanum Brid. and C. kindbergii (Ren. et Card.) Grout and concluded that C. kindbergii was not a variety of C. amercanum as has long been thought (Horton and Vitt 1976), but a separate species. Electrophoretic and morphological differences indicate a linkage disequilibrium between the two species. This conclusion is further supported by the fact that the species are often found growing together which indicates that they have become reproductively isolated. In fact, C. kindbergii plants from one site are more like C. kindbergii plants from another site, than like C. americanum plants at the same site. De Vries et al. (1989) found moderate to high levels of gene diversity in populations of Racopilum species that were comparable to phanerogam populations. Dewey (1988) was able to confirm the distinction between Riccia dictyospora Howe and R. mcalisteri Howe with electrophoresis although genetic variability in the genus was quite low. He suggested that other species in the genus have been classified based on phenotypic differentiation rather than genetic divergence. Boisselier-Dubayle and Bischler (1989) found a good correlation between habitat and electrophoretic data in Marchantia polymorpha L. They found that plants growing in urban and natural wet habitats differed genetically and within the wet plant populations there were also two biotypes. Innes (1990) found high interpopulational genetic variation in Polytrichum juniperinum Hedw., although variation within populations was low, indicating that mating occurs primarily among members of the same area and that gene flow distances are relatively short compared to other mosses with high variation within populations. High levels of gene diversity have also been detected within and among populations of Sphagnum pulchrum (Braithw.) Warnst. with the highest genetic distance between populations at 0.42 (Daniels 1982).

Cummins and Wyatt (1981) were the first to determine the degree of genetic variability among individual plants within samples of a population. Atrichum angustatum (Brid.) B.S.G. was found to be electrophoretically polymorphic within and among populations and within 5 X 5 cm samples. The degree of variability detected within and among populations was comparable to variabilities in angiosperms and animals. Meagher and Shaw (1990) found genetic variation within distinct clumps (ca. < 60 cm^2) of Climacium americanum, although the majority of variation in this moss was among clumps. Probably the most interesting study in this area was done by Wyatt et al. (1987 and 1989) in which levels of gene diversity were detected in populations of Plagiomnium ciliare (C. Muell.) Kop. that were comparable to those of the conifers that have the most highly recorded genetic diversities of all vascular plants (Ennos 1990). Not only did these workers find high levels of variation between and within populations, but they also found genetic heterogeneity in groups of five plants from 25 cm^2 samples of moss, although as of yet, there is no understanding how the gene diversity of samples of populations relate to the gene diversity of the population as a whole. Finally, Wyatt et al. (1989a) found that there was more gene diversity in mosses from old growth forests than in secondary growth forests possibly indicating that a genetic bottleneck had probably taken place not too distantly in the past.

Evidently the theories that state that bryophytes have slow rates of evolution because they are depauperate in genetic variability may be rejected based on the above studies of electrophoretically detectable variation, and yet we know that some bryophytes have not changed substantially in their morphology since the early Tertiary (Janssens et al. 1979). What are the explanations for this apparent discrepancy? It has been suggested that the genes that are detected and quantifed through electrophoresis are selectively neutral and are not linked with genes which determine fitness, therefore while the electrophoretically detectable variation is high the actual genetic variation involved in

evolution may be low (Brown et al. 1989; de Vries et al. 1989; Dewey 1989; Ennos 1990; Nei 1988; Szweykowski 1984; Yamazaki 1981; and Zielinski 1986). If the high allozyme heterogeneity detected in bryophytes describes genes which are not affected by natural selection, then we can conclude that the rate of directional evolution in bryophytes is quite low as the evidence suggests. We can also conclude that the potential to evolve in bryophytes is high evinced by high variation in some traits (Zielinski 1986), and we can conclude, although less securely, that natural selection is working to maintain bryophyte traits controlling fitness rather than to change them. Natural selection will select strongly against deterious mutations, but if the mutations are selectively neutral they will remain in the population. If high electrophoretically detectable gene diversity is selectively neutral and selected traits are relatively constant, centripetal or stabilizing selection is in action.

Other explantations for the high electrophoretically detectable genetic variability in bryophytes are based on mutation rates. Mutations of characters associated with fitness would be strongly selected against in haploid organisms, but mutations of selectively neutral traits may be retained in the population with no effect on the individual members. If electrophoresis detects only selectively neutral gene diversity, then a great deal of the variation may be due to mutation. Shaw (1990) found a substantial amount of variation in the morphology, germination percentage, gametophytic growth, and copper tolerance in Funaria hygrometrica Hedw. plants derived from the same genetic individual, indicating that mutation occurs often and at different stages in the development of the moss plant. Extremely high mutation rates have been detected in some plants; one in every 80 Y chromosomes per generation mutates for centromere relocation in Rumex acetosa L. (Parker and Wilby 1989). Furthermore, there is evidence that some mutations may in fact be biological responses to environmental stimuli, rather than simply random events (Eckhardt -Schupp 1989; Lenski 1989; and Roth et al. 1989). Finally, mutations may be particularly important in long-lived perennials, like some moss species, as each apical bud

has more chance of undergoing mutation than in short lived species. Apical bud mutations lead to gene diversity not only in the population, but also within the individual (Daniels 1982; Fahselt 1989; and Nickrent and Wiehs 1989).

Alternatively, electrophoretically detectable genetic variation may be indicative of all genetic variation in the population or species. An obvious explanation for high gene diversity within a population is that each population is made up of individuals from a number of different spores. Asexual reproduction maintains genotypes in the population and fine-grained, density independent mortality of stems would prevent any genotype from dominating the population (During and van Tooren 1987). Some researchers suggest that bryophytes and other clonal organisms show high degrees of genetic variation because they have been naturally selected for by a very fine grained micro-habitat mozaic, and within each micro-habitat the genotypes are relatively homogenous (Cummins and Wyatt 1981; Daniels 1982; Dewey 1989; Ellstrand and Roose 1987; Spieth 1975; and Wyatt et al. 1989a). Daniels found that populations of Sphagnum recurvum var. mucronatum (Russ.) Warnst. (1985a) and S. compactum DC. ex Lam. et DC. (1985b) were more genetically complex in habitats that were variable in terms of water level and chemistry than in habitats that are relatively stable through time, indicating that a connection may exist between environmental selective pressures and electrophoretically detectable genetic variation. Gene diversity may be caused through differential natural selection on different developmental stages; the moss protonema, no doubt, has different selective pressures acting on it than has the moss sporophyte (Dewey 1989; de Vries et al. 1983; and Zielinski 1986). Maravolo et al. (1967) found that the thallus and stalk of Marchantia polymorpha expressed different enzyme phenotypes from the antheridophore disks.

The bands which are produced through electrophoresis are considered phenotypes which, theoretically, could be plastic in their response to the environment. Zielinski (1986) found that peroxidase and esterase banding phenotypes in Pellia endiviifolia

differed in band intensity among populations in the field, but when the same populations were cultured in the laboratory for two to six months the differences were not detected. Differences among populations included staining intensities of known bands that were so low that the bands were not detected and could have been interpreted as null alleles. Cronberg (1989) found allozyme differences in one enzyme system between Sphagnum capilifolium (Ehrh.) Hedw. and S. rubellum Wils., but he could not conclude that they were actually genetically different because the two species lie on either end of the mire-margin gradient and the electrophoretic phenotype difference may have been environmentally induced.

High genetic variabilities in mosses could result from ancient or recent polyploidy (de Vries et al. 1989; and Szweykowski 1984). Plagiomnium ciliare is suspected of undergoing polyploidy long in the past and has since been silenced at a number of loci (Wyatt et al. 1989a). Longton (1976) has suggested that the majority of mosses are autopolyploids which implies that the arguement of mosses posessing low genotype frequencies because of their dominant haploid state can be discarded in many cases as polyploidy allows for genetic buffering.

A final explanation for the unexpected high levels of genetic heterogeneity in bryophytes is that gene flow distances may be longer than expected. Spore numbers per capsule are so large (between several hundred thousand to two million or more (Longton and Miles 1982)) that if even only a very small fraction of the spores produced in one population was carried extrordinarily far, it could account for the gene diversity found in another population (de Vries et al. 1983; and Wyatt 1982). Moss fragments may also have longer dispersal rates than we now know.

Most investigators have found that genetic distances among populations of brophytes do not relate in any way to spatial distances. Such patterns can provide information on the history or evolution of a species (Crouau-Roy 1989a). Dewey (1989)

found no geographic arrangement in three genotypes of Riccia dictyospora. Innes (1990) found no relationship between genetic and spatial distances in populations in Polytrichum juniperinum and neither did Wyatt et al. (1989a) in Plagiomnium ciliare, nor deVries et al.(1989) in Racopilum species. Speith (1975), however, found similarities between the patterns of genetic distance and the patterns of spatial distance only when he expanded the range of his studies. He concluded that in a small area the microhabitats in which Neurospora intermedia (a haploid fungus) occurs are more the same than different. Differing selective pressures may only be evident over wide geographical ranges.

In this study Meesia triquetra, a rare, rich fen indicator species of high fidelity, is examined for its gene diversity. Gene diversity may be used as an indicator of evolutionary potential since evolution is dependent on gene diversity. There are three objectives to this study: 1) to quantify gene diversity of M. triquetra and to relate the degree of variability to gene diversity studies in other mosses and organisms, 2) to determine whether gene diversity in M. triquetra is related to latitude, and 3) to determine to what extent the gene diversity of relatively small samples of fens reflect the genetic structure of their fens of origin, and to determine how the relationship between sample and fen varies with latitude.

Methods

Study regions

Meesia triquetra occurs from northernmost Ellesmere Island and Alaska, south to Montana, California, Wisconsin, Pennsylvania and Newfoundland (Montagnes 1990). Three regions in northern and western Canada were chosen along an 3000 km Arctic-Boreal gradient: boreal Alberta, the forest tundra (subarctic) in the Yukon Territory, and the high arctic on Ellesmere Island, N.W.T. The Yukon region is approximately half way between the boreal and arctic regions.

The boreal region is located between Edson and Nordegg, Alberta (between 55° 35' N 116° 26' W and 52° 50' N 116° 05' W). This is a wooded area of the Alberta plain at the eastern edge of the Rocky Mountain foothills. It is underlain by Tertiary sandstones and shales, with a cover of hummocky ground moraine deposited by the Cordillerian glacier during the Wisconsinan period. The till is stoney with limestone blocks (Clayton et al. 1977a). Elevations rise between 1200 and 1800 m above sea level (Drinkwater et al. 1969). This area is also part of a sand dune complex formed by glacial Lake Edson (Slack et al. 1980).

The climate of the boreal region is cool temperate with a July mean monthly temperature of 14.4°C. It has a frost free period (number of days between the last frost in the spring and the first frost in the fall) of approximately 80 days and receives an average annual precipitation of 533 mm, with 305 mm falling during the frost free period (Alberta Environment 1988; and Drinkwater et al. 1969).

Tree covered hills, mainly dominated by Picea glauca (Moench) Voss, P. mariana (Mill) BSP., and Pinus contorta Loudon associations and occasional Populus tremuloides Michx., stands alternate with abundant ponds and open mires in low lying areas (Clayton et al 1977a; Drinkwater et al.1969; Slack et al. 1980).

Five fens (sites) were selected from this region. One was located along a pond margin, five km south of highway 16, on the east side of highway 47 (Plate III-1), two were in small basin fens (one on the west side of the Forestry Trunk Road, five km south of Pembina River crossing, and the other on the south side of the Cardinal River Road, 10 km west of the junction with the Forestry Trunk Road), and two were part of larger peatland complexes (one on the west side of highway 40, 15 km south of Robb, 1 km south of a provincial campsite, and the other on the west side of the Forestry Trunk Road, 10 km southeast of the junction with the Cardinal River Road).

The subarctic region is located along the Dempster Highway between km 96 and 190 (between 64° 30' and 65° 30'N at approximately 138° 50' W). The Dempster Highway is the link between Dawson City, YT. and Inuvik, N.W.T. It runs along river valleys and hill crests of unmanaged crown land.

The section of Highway used in this study runs over the Porcupine Plateau which consists of sedimentary bedrock of Paleozoic carbonates. The Plateau lies between the Richardson mountains to the northeast and the Ogilvie mountains to the southwest. Elevations range from 500 to 1000 m above sea level in rolling hills. Soils are humid, stoney or sandy aluvial deposits and glaciofluvial till. This region remained unglaciated throughout the Pleistocene (Clayton et al. 1977b).

The climate of this region is substantially cooler than that of the boreal region, with mean monthly temperatures in the negative twenties in January and of approximately 14°C in July. Annual precipitation is about 350 mm. The average annual frost free period lasts 60 days (Alberta Environment 1988; and Bryson and Hare 1974).

The vegetation on the Porcupine Plateau is forest tundra; alternating stands of stunted Picea glauca and P. mariana forests, and large stretches of open tundra. Forested mires have developed on poorly drained areas underlain by permafrost (Stanek et al. 1981; and Kojima and Brooke 1985).

Five fens (sites) were chosen for study in the subarctic region. One was along a pond margin at km 141, on the east side of the Dempster Highway, one was located near a wide-spread stream in the open tundra at km 96 on the west side of the Dempster Highway, one was located in a swampy Betula-Salix stand at km 190 on the east side of the Dempster Highway, and the other two were located in small basins adjacent to treed areas (one at km 175 on Dempster Highway (Plate III-2), and the other at km 183 on the west side of the Dempster Highway).

The third region is located in the high arctic at Princess Marie Bay on Ellesmere Island, N.W.T. (79° 29' N, 75° 47' W). It is an estuary lowland which expands north for 20 km and was 5 km wide. The lowland is banked on either side by folded mountains of sedimentary limestones and sandstones laid down in the Ordovician and Silurian periods. The region was glaciated during the Pleistocene and experienced postglacial marine submergence. Isostatic uplift is still occurring at a substantial rate (Williams et al. 1980). All sites were located between 15 and 50 m above sea level. Soils in this area are mainly poorly developed regosols of humid loamy glacial till or fluvial deposits (Clayton et al.1977b).

Climate studies of the Princess Marie Bay area are few. The limited records show mean monthly July temperatures of 6.6°C, a frost free period of 37 days (Williams et al. 1980) and the total precipitation for the months of July and August of 26.1 mm (G. Henry unpubl. data). The Princess Marie Bay lowland is considered a polar desert .

The vegetation of Princess Marie Bay is controlled, in the most part, by soil moisture. The land ranges from barren, or near barren, clay badlands, exposed rock and scree occasionally colonized by Dryas integrifolia M. Vahl, Saxifraga oppositifolia L., and Salix arctica Pall., to slightly more vegetated stable terraces which have, in addition to the above species, species of Carex, Lesquerella, and Braya. Species richness and vegetative cover is highest along seepage slopes and in wet sedge meadows in low lying areas (Williams et al. 1980).

The five sites in this area were located within 15 km of each other. Two of the sites were located on patterned outflows of ponds (one on the east side of lowland, one km north of the coast, and the other on the east side of lowland, on a 20 m terrace, six km north of the coast), two were located in wet meadows (one was the most extensive meadow in lowland, seven km north of the coast (Plate III-3), and the other is between a large hill and the coloured mountain, 16 km north east of coast.), and the last was located

along a gently inclined seepage slope on east side of lowland, on a 15 m terrace, six km from the coast.

Fifty collections of live moss (approximately 24 cm^2, 7 cm deep) hereafter refered to as demes, containing at least ten Meesia triquetra stems, were collected from each of the fifteen sites. Thus, collections were made in a nested fashion with stems within each of 50 demes from each of five sites from each of three regions. Deme collections were made no less than one metre apart. The demes were placed in plastic bags and kept cool until use when they were placed in plastic greenhouse cell trays and left to grow in the growth chamber. The trays were set in a 4 cm deep water bath to ameliorate temperature differences due to lighting on the growth bench. The lighting was held constant with 16 hours of light at an intensity of 300 μ mol s^{-1} m^{-2} per 24 hour period. The water bath had daily maximums of 18°C and daily minimum temperatures of 10°C. Relative humidity was held at 65%. Every day the trays were watered with distilled, dionized water.

In order to determine the gene diversity of Meesia triquetra as a species, and to determine whether the gene diversity of this moss varies with latitude (objectives 1 and 2), one stem from each of thirty randomly chosen demes per site was assayed for enzyme phenotype through electrophoresis after the methods of Bayer (1988). In order to determine how the gene diversities of the demes relate to the gene diversities of their sites of origin, and to determine how this relationship varies over an arctic-boreal gradient (objective 3), one deme was chosen from each region, and thirty stems from each deme were assayed for enzyme phenotype.

The stems were ground with mortar and pestle on ice in two drops of an ice-cold extraction buffer: 1 M Tris-HCl, pH 7.5, 4.0 mM 2-mercaptoethanol, 1.0 mM EDTA (disodium salt), 0.2 M sucrose, 0.6% polyvinyl-polypyrrolidone (5:1 ratio of 40K:360K m.w.), 2.0% PEG (8K m.w.), 0.1% BSA, and 0.002 M ascorbic acid. The extract was absorbed on two filter paper wicks which were frozen at -20°C for 24 hours and then

loaded into 12.5% starch gels. Malate dehydrogenase (MDH), phosphoglucoisomerase (PGI), phophogulcomutase (PGM), and aldolase (ALDO), were resolved on a system consisting of a gel buffer of 0.016 M L-histidine (free base) and 0.002 M citric acid·H_2O (pH 6.5), and an electrode buffer of 0.065 M L-histidine (free base) 0.007 M citric acid·H_2O (pH 6.5). Glucose-3-phosphate dehydrogenase (G3PDH), glutamate oxaloacetate transaminase (GOT), alcohol dehydrogenase (ADH) and triosephosphate isomerase (TPI).were resolved on a system composed of a gel buffer consisting of one part 0.038 M lithium hydroxide·H_2O-0.188 M boric acid (pH 8.3), and 9 parts 0.045 M Tris-0.007 citric acid (pH 8.4), with the electrode buffer consisting only of the lithium borate constituent.

Isozyme variation was used to determine gene diversity ($\underline{H}$, Nei 1973) in Meesia triquetra within and among sites from the three regions and among the three demes from the three regions with the GENESTAT program (Whitkus 1985). Also the average gene diversity of each site was calculated as $(\Sigma \underline{H}_{ik})/n$; where $\underline{H}_{ik}$ is the gene diversity of the i^{th} site at the k^{th} locus and n is the total number of loci. These values were regressed against latitude to determine whether the overall gene diversity in sites of M. triquetra varies with latitude with the MacIntosh program CRICKETGRAPH (Raferty and Norling 1987). Principal components analysis (PCA) was performed on the data to determine the major axes of variation and to examine any resulting phytogeographic pattern of sites with the NTSYS-pc program (Rohlf 1987). Allele frequencies were used to determine the genetic distances ($\underline{D}$) and identities ($\underline{I}$) (Nei 1972) between regions, between sites, and between demes and their sites of origin. Phenograms were made from the values of $\underline{I}$ to present this data graphically with NTSYS-pc.

Results

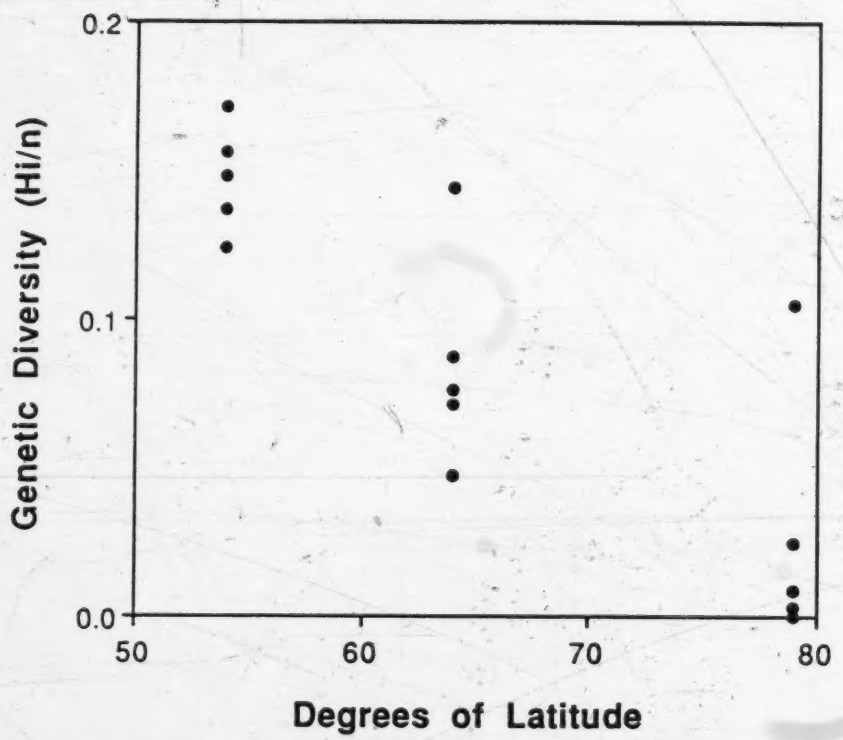
Enzyme band interpretation is facilitated because only one allele can be carried at each locus due to the haploid condition of Meesia triquetra gametophytes. The chromosome number of M. triquetra is n = 10 (Steere 1954a, 1954b; and Inoue 1979) although, Inoue (1979) reported a diploid number (n=20) from northern Alaska. The 18 putative isozymes (and their allozymes) detected are: MDH-1 (A and B), MDH-2 (A to C), MDH-3 (A to C), PGI-1 (A), PGI-2 (A and B), PGI-3 (A to C), PGM-1 (A), PGM-2 (A), PGM-3 (A to C), TPI-1 (A and B), TPI-2 (A and B), GOT-1 (A), G3PDH-1 (A), G3PDH-2 (A and B), ALDO-1 (A and B), ALDO-2 (A to C), ADH-1 (A and B), and ADH-2 (A and B). ADH-1 and G3PDH-1 were often not expressed in which cases they were not considered in the analysis. Allele frequencies are listed in Appendix 4.

Total gene diversity (H_t) of the regions and intra-site gene diversity within regions (H_S) show a decreasing trend with increasing latitude (Table VI-1); however, inter-site gene diversity (D_{ST}) is highest in the subarctic populations, lowest in the high arctic populations and intermediate in the boreal sites. Five of the 18 loci expressed polymorphism in the high arctic sites, nine loci showed variation in the subarctic sites, and 11 loci showed variation in the boreal sites. Most of the loci that were polymorphic in the North were also variable in the South; exceptions are Adh-1, which was polymorphic in the high arctic and boreal sites but not in the subarctic sites, and Pgi-2 and Tpi-2 which varied in the subarctic sites but not in the boreal sites. The average gene diversity for each site shows a relationship with latitude (Fig VI-1). Regression analysis indicates that 70% of the variation in these data can be accounted for by the latitudinal gradient at a significance level of $p << 0.005$. This graph (Fig. VI-1) however, illustrates the relatively high D_{ST} value for the subarctic sites; the subarctic sites are far more widely distributed along the diversity axis than sites from the other two regions.

Table VI-1. Total gene diversity (H_t), within subpopulation gene diversity (H_s), and between subpopulation gene diversity (D_{st}) at the species, region, and deme levels of nesting in Meesia triquetra.

	H_t	H_s	D_{st}
All sites	0.1509	0.0823	0.0685
High Arctic	0.0795	0.0567	0.0227
Subarctic	0.1446	0.0744	0.0702
Boreal	0.1805	0.1310	0.0495
Demes	0.1528	0.0447	0.1081

Fig. VI-1. Bivariate plot of gene diversity of 15 individual sites versus degrees of latitude of site locations.

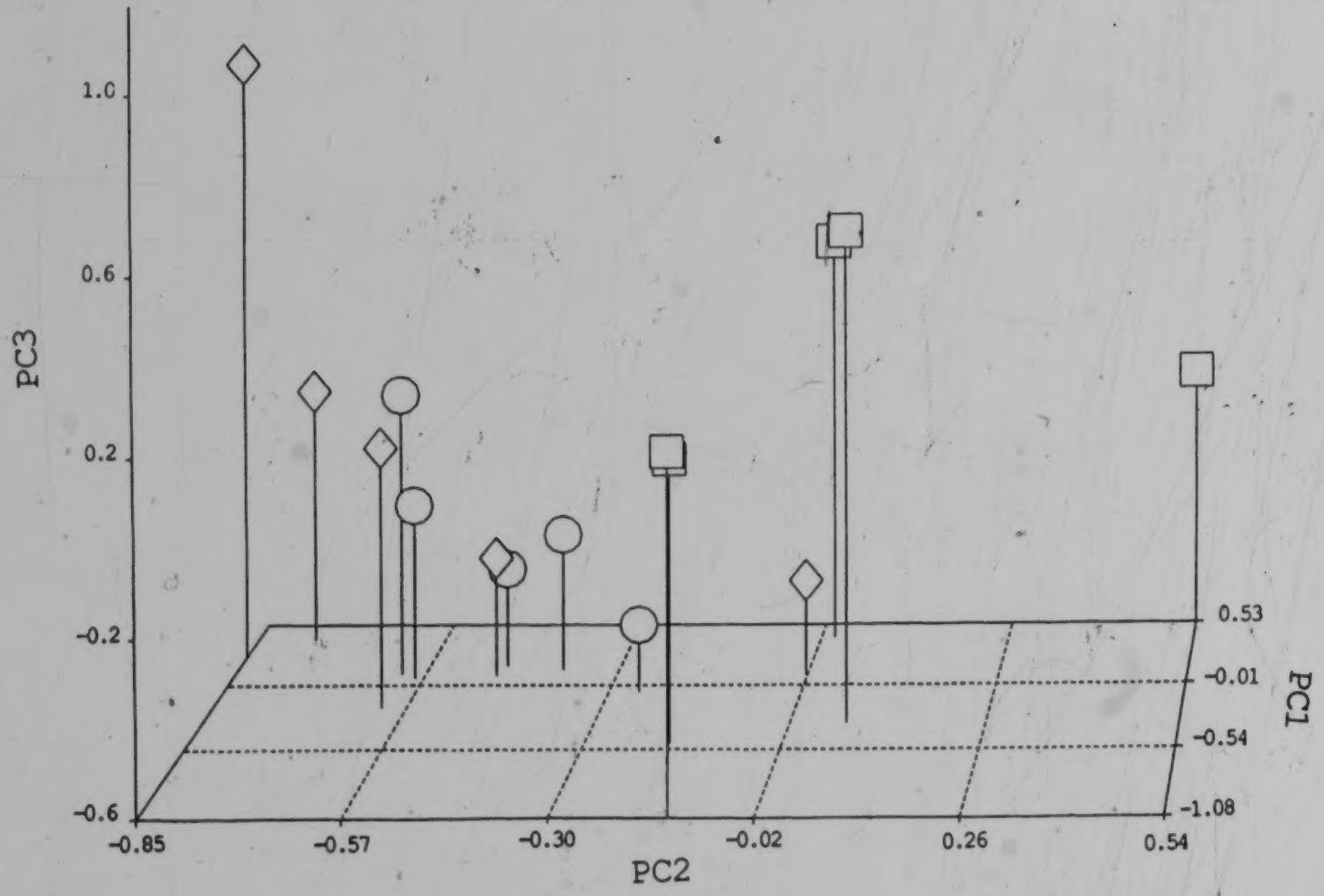

0.2
0.1
0.0
Genetic Diversity (Hi/n)
50
60
70
80
Degrees of Latitude

Results from the PCA (Fig. VI-2.) show the high arctic sites in a small area with high positive principal component (PC) 1 and high negative PC2 and PC3 loadings, indicating a strong influence from Tpi-1^{a}, Tpi-1^{b}, and Adh1-^{b} alleles. Conversely the boreal sites are scattered across PC1, but have high PC 2 and PC3 loadings, indicating strong influence from Mdh-1^{a}, Mdh-1^{b}, Pgm-3^{a}, Pgm-3^{b}, Aldo-1^{a}, and Aldo-1^{b} , and moderate influence from Mdh-2^{c}, Pgi-2^{a}, Pgi-2^{b}, and G3pdh-2^{a} . Finally, the subarctic sites are located high on the PC1 axis, but throughout the PC2 and PC3 axes. The subarctic and high arctic sites overlap considerably, while both are well separated from the boreal sites (Fig. VI-2).

Genetic similarities (I) between pairs of sites ranges from 0.900 - 1.00 (Table VI-2). A UPGMA phenogram (Fig. VI-3) based on all pairwise comparisons of I values from the 15 sites (Table VI-2) shows little pattern, contrary to the expected clustering of sites into regions. A phytogeographic arrangement was no clearer in phenograms using several other clustering methods (WPGMA using Spearman's rank coefficient or centroids, and single or complete linkage). A phenogram of the average genetic identity of regions shows that the subarctic and high arctic regions are far more similar to each other than they are to the boreal region (Fig. VI-4) which is similar to the relationships portrayed by the PCA in Fig VI-2.

All analyses of sites that included the individual deme assays were greatly affected by the boreal deme that contained plants with a Mdh-3 allele that was slower than any other allele at that locus. A PCA of all the sites and the three individual demes shows that the populations of the three regions are well separated on both axes, but they are pushed far to the left by the individual boreal deme (Fig. VI-5). The subarctic deme is located close to the vicinity of the high arctic sites in the ordination and the high arctic deme is immediately adjacent to the high arctic sites, but it is farther from the high arctic sites than is the subarctic deme.

Fig. VI-2. Principal components analysis of allele frequency variation in 15 sites (squares represent boreal sites, diamonds subarctic sites, and circles high arctic sites).



141a

Fig. VI-3. UPGMA phenogram based on Nei's genetic identity of 15 sites (AB = boreal sites, YT = subarctic sites, and EL = high arctic sites).

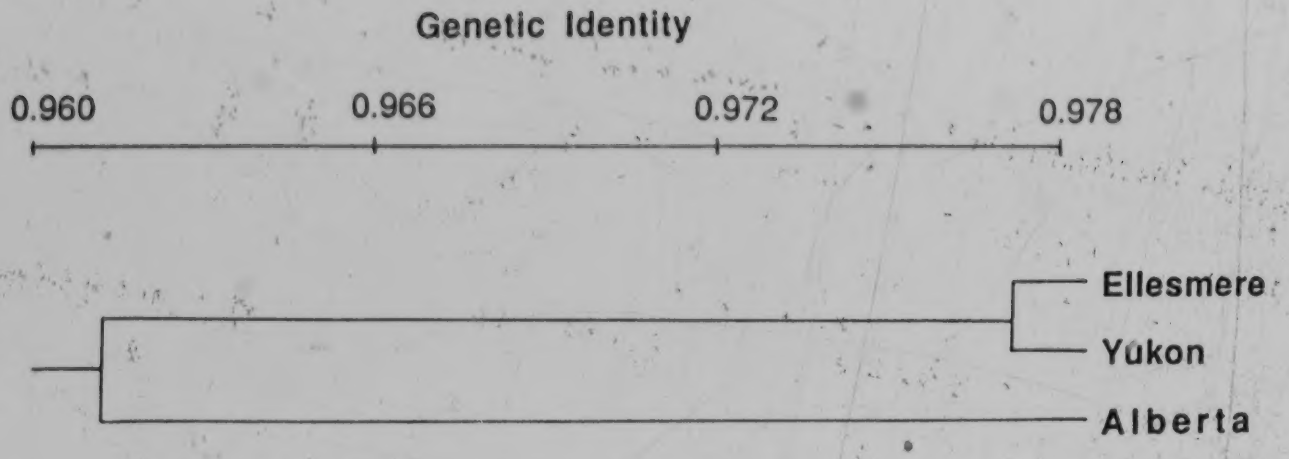

Genetic Identity
0.960
0.966
0.972
0.978
Ellesmere
Yukon
Alberta

Table. VI-2 Genetic identities (above) and Distances (below) among populations of Meesia triquetra from along an arctic-boreal gradient. (EL = high arctic sites, YT = subarctic sites, and AB = boreal sites).

Population	EL1	EL2	EL3	EL4	EL5	YT1	YT2	YT3
EL1	--	0.9997	0.9527	0.9672	0.9332	0.8922	0.9029	0.9287
EL2	0.0003	--	0.9483	0.9613	0.9280	0.9306	0.8869	0.9165
EL3	0.0484	0.0531	--	0.9793	0.9966	0.8750	0.9874	0.9924
EL4	0.0333	0.0395	0.0209	--	0.9731	0.8484	0.9470	0.9781
EL5	0.0692	0.0748	0.0034	0.0273	--	0.8636	0.9289	0.9924
YT1	0.1140	0.0719	0.1335	0.1644	0.1466	--	0.8014	0.8161
YT2	0.1022	0.1200	0.0127	0.0545	0.0738	0.2214	--	0.9568
YT3	0.0740	0.0871	0.0076	0.0221	0.0077	0.2032	0.0442	--
YT4	0.0876	0.1006	0.0784	0.0777	0.0747	0.0858	0.1361	0.0849
YT5	0.0033	0.0029	0.0862	0.0447	0.1121	0.0003	0.1295	0.0914
AB1	0.0630	0.0729	0.0094	0.0796	0.0384	0.1853	0.0571	0.1021
AB2	0.0476	0.0514	0.0175	0.0373	0.0249	0.1379	0.0950	0.0304
AB3	0.0245	0.0279	0.0428	0.0737	0.0741	0.1511	0.0848	0.1335
AB4	0.0351	0.0403	0.0962	0.0491	0.1178	0.1646	0.1158	0.0878
AB5	0.0512	0.0588	0.1070	0.0910	0.1950	0.1367	0.1447	0.1600

	YT4	YT5	AB1	AB2	AB3	AB4	AB5
EL1	0.9162	0.9967	0.9389	0.9535	0.9758	0.9655	0.9501
EL2	0.9043	0.9971	0.9297	0.9499	0.9725	0.9605	0.9429
EL3	0.9246	0.9174	0.9906	0.9826	0.9581	0.9083	0.8986
EL4	0.9252	0.9563	0.9235	0.9633	0.9289	0.9521	0.9130
EL5	0.9280	0.8940	0.9624	0.9754	0.9285	0.8889	0.8229
YT1	0.9177	0.9997	0.8309	0.8712	0.8598	0.8482	0.8722
YT2	0.8727	0.8786	0.9445	0.9094	0.9187	0.8907	0.8653
YT3	0.9186	0.9127	0.9029	0.9701	0.8750	0.9160	0.8522
YT4	--	0.9514	0.9058	0.9062	0.9067	0.8684	0.8945
YT5	0.0499	--	0.8122	0.9410	0.8846	0.9734	0.9428
AB1	0.0990	0.2081	--	0.9617	0.9704	0.8574	0.8418
AB2	0.0985	0.0608	0.0391	--	0.9471	0.9481	0.9251
AB3	0.0980	0.1226	0.0301	0.0544	--	0.8978	0.9161
AB4	0.1411	0.0270	0.1539	0.0600	0.1078	--	0.9642
AB5	0.1115	0.0589	0.1722	0.0779	0.0877	0.0364	--

Fig. VI-4. UPGMA Phenogram based on Nei's genetic identity of sites from three ecoclimatic regions

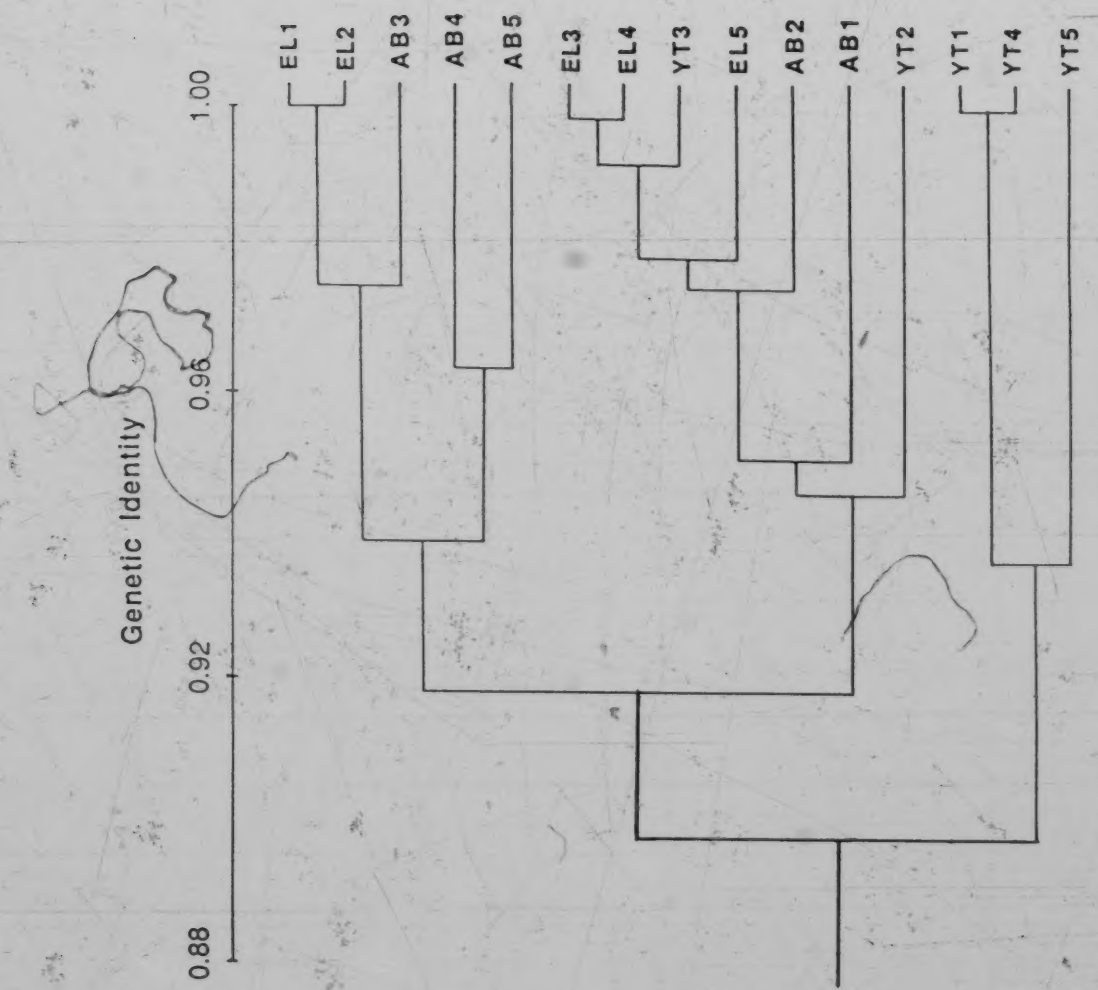
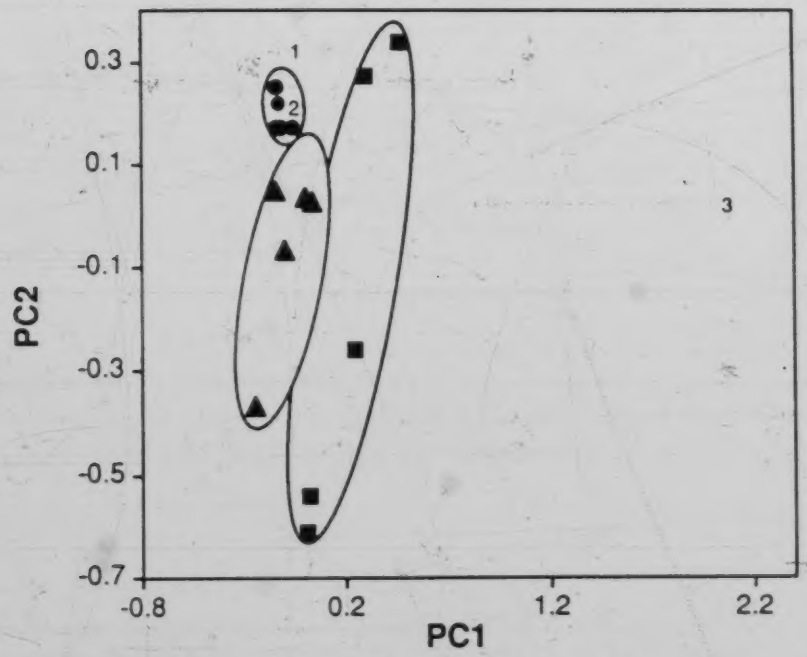

Genetic Identity
1.00
0.96
0.92
0.88
EL1
EL2
AB3
AB4
AB5
EL3
EL4
YT3
EL5
AB2
AB1
YT2
YT1
YT4
YT5

Fig. VI-5. Principal components analysis of 15 sites and of three demes from the sites (1 represents the deme from an high arctic site, 2 from a subarctic site, and 3 from a boreal site).



■ boreal sites
▲ subarctic sites
● high arctic sites
1 high arctic deme
2 subarctic deme
3 boreal deme

The genetic identities of the three individually assayed demes have a pattern similar to that shown by regions. The boreal deme is much farther removed from the other two demes than the boreal region is from the other two regions because of the unique Mdh allele in the boreal stems. The boreal deme showed polymorphism in eight of 16 isozymes, whereas the subarctic deme was polymorphic at only one isozyme of 14 examined and the high arctic deme was monomorphic at all 17 loci examined. Total gene diversity (H_t) in the three demes together is very close to that of the species as a whole (Table VI-1), which indicates that only a few small samples of the species can reflect the gene diversity of the species, and that the clone size in this moss is much more finely grained than was expected from a predominantly clonal plant. However, D_{st} contributes more greatly to the H_t value for the demes than it does for the H_t value of the species as a whole. There is a trend of increasing genetic identity (I)between the deme and its site of origin with latitude: I of the boreal deme and its site of origin is 0.8262, of the subarctic deme and its site of latitude is 0.9279, and of the high arctic deme and its site of origin is 0.9722.

Discussion

Genetic diversity

Values of gene diversity (H_t) for Meesia triquetra fall well within the range of those reported for several Racopilum species, Plagiomnium ciliare, and Conocephalum conicum (Table VI-3). All of the bryophytes listed are dioicous except for monoicous R. tomentosum (Hedw.) Brid. Dioicous species would be expected to have higher genetic diversity than monoicous species because dioicous plants are obligate outcrossers, whereas monoicous plants are able to self fertilize; however, the gene diversity of R. tomentosum does not greatly differ from any of the other mosses.

Table VI-3. Genetic diversities (H_t) within species.

Species	H_t	Author
Mosses		
Meesia triquetra	0.151	this paper
Racopilum strumiferum	0.18	de Vries et al. 1989
Racopilum tomentosum	0.17	de Vries et al. 1989
Racopilum intermedium	0.08	de Vries et al. 1989
Racopilum capense	0.08	de Vries et al. 1989
Racopilum spectabile	0.26	de Vries et al. 1983
Racopilum cuspidigerum	0.26	de Vries et al. 1983
Plagiomnium ciliare	0.177	Wyatt et al. 1989a
Liverworts		
Conocephalum conicum	0.167	Yamazaki 1981
Pellia neesiana	0.025	Zielinski 1987
Pellia borealis	0.045	Zielinski 1987
Vascular plants		
Antennaria rosea	0.183	Bayer 1989
Hordeum spontaneum	0.003	Nevo et al. 1979
Phlox cuspidiata	0.008	Levin 1978
Gaura longiflora	0.074	Gottlieb and Pilz 1976
Picea abies	0.370	Lundkvist 1979
General - Vascular plants		
Autogamous	0.291	Loveless and Hamrick 1984
Mixed mating	0.242	Loveless and Hamrick 1984

Predominantly outcrossing	0.251	Loveless and Hamrick 1984
Hermaphroditic	0.284	Loveless and Hamrick 1984
Monoecious	0.224	Loveless and Hamrick 1984
Dioecious	0.155	Loveless and Hamrick 1984
Obligate apomixis	0.172	Loveless and Hamrick 1984
Facultative apomixis	0.356	Loveless and Hamrick 1984
Sexual	0.261	Loveless and Hamrick 1984

The two Pellia species reported by Zielinski (1987) and other gene diversity records for liverworts cited by Wyatt et al. (1989b) indicate that overall, hepatics may have lower gene diversities than mosses. Khanna (1964) argued that since liverworts, compared to mosses, have a smaller number of species, less variation in chromosome number, less effective spore dispersal mechanisms, and are less ecologically successful, that liverworts have a slower rate of evolution than mosses. Lower genetic diversities in liverworts would also support Khanna's views, but the evidence is scant.

Meesia triquetra has a H_t value much higher than selfing vascular plants such as Hordeum spontaneum C. Koch (Nevo et al. 1979) or Phlox cuspidata Scheele (Levin 1978) and even higher than the outcrossing Gaura longiflora Spach (Gottlieb and Pilz 1976), although M. triquetra has a much lower H_t value than Picea abies (L.) Karst (Lundkvist 1979). In terms of average genetic heterogeneity, mosses appear to be slightly more homogenous than vascular plants (Loveless and Hamrick 1984). Gene diversity in M. triquetra is close to that of apomictic vascular plants, even though M. triquetra is an obligate outcrosser, and also close to the values reported for dioecious vascular plants which are more similar to the actual case; M. triquetra being dioicous. Dioecious plants are low in gene diversity presumably because many resort to vegetative reproduction to offset the spatial reproductive barrier, as does M. triquetra. Only Racopilum spectabile Reinw. et Hornsch. and R. cuspidigerum (Schwaegr.) Aongstr. gene diversity values are near the average values reported for outcrossing or sexual plants, and none of the mosses reported has diversities as high as those reported for autogamous, hermaphroditic, or facultatively apomictic plants (Loveless and Hamrick 1984).

Values of I among sites of Meesia triquetra are higher than among populations of other moss species reported, and the range of I in M. triquetra is narrower than in other mosses (Table VI-4). Mosses appear to have remarkably wide ranges of I among populations, for instance, Racopilum capense C. Mull. ex Broth. populations range from

Table VI-4. Genetic identities (I) among populations.

Species	Identity	Author
Mosses		
Meesia triquetra	0.900 - 1.000	this paper
Plagiomnium ciliare	0.813 - 0.998	Wyatt et al. 1989a
Racopilum spectabile	0.853 - 0.899	de Vries et al. 1983
Racopilum strumiferum	0.880 - 0.960	de Vries et al. 1989
Racopilum tomentosum	0.960 - 0.990	de Vries et al. 1989
Racopilum capense	0.520 - 0.990	de Vries et al. 1989
Sphagnum pulchrum	0.657 - 0.967	Daniels 1982
Sphagnum recurvum var. *mucronatum*	0.430 - 0.864	Daniels 1985a
Vascular plants		
Dedeckera eurekensis	0.855 - 0.974	Nickrent and Wiens 1989
Senecio flavus	0.857 - 0.984	Liston et al. 1989
Antennaria rosea	0.718 - 0.990	Bayer 1989
Coreopsis nuecensis	0.900 - 0.990	Crawford and Smith 1982
Elymus canadensis	0.960	Sanders et al. 1979
Pseudotsuga mensiesii	0.990	Yeh and O'Malley 1980
Picea abies	0.980	Lundkvist 1979
Sullivantia hapemanii	0.900 - 1.000	Soltis 1981
Hordeum spontaneum	0.890	Nevo et al. 1979
Gaura longiflora	0.990	Gottlieb and Pilz 1976

Animals

Speonomus hydrophilus	0.952 - 0.981	Crouau-Roy 1989a
Speonomus zophosinus	0.960 - 1.000	Crouau-Roy 1989b
Didelphis virginiana	0.904 - 0.955	Kovacic and Guttman 1979

0.520 to 0.990 in identity (de Vries et al. 1989) and those of Sphagnum recurvum var. mucronatum range from 0.430 to 0.864 in identity (Daniels 1985a), whereas within many vascular plant populations, I values among populations are rarely lower than 0.700 and animals such as the cave dwelling beetle, Speonomus zophosinus Saulcy, and the Opossum, Diadelphis virginianum Kerr, do not have values of I among populations below 0.900. Genetic identities among populations within some bryophyte species are as low as most values of I between vascular plant species. Presumably the large differences among populations in mosses is a result of clonal growth within populations where single genotypes may be common in one population and rare or non-existant in another. The sites used in this study are not as widely divergent in I values as other mosses indicating that the variation in this moss is relatively consistent thoughout its range which may imply a high degree of gene flow.

Although M. triquetra has a low genetic variability, both in gene diversity and in the range of I values among populations relative to other moss species, this moss is comparable in both these indices to many vascular plants and animal species. Genetic variability is required for evolution before any ecological, spatial, or temporal reproductive barriors can be effective in leading to speciation. Evidently, if M. triquetra and other mosses are evolving slowly compared to other organisms, it is not because they have depauperate genotypes.

Genetic variation with latitude

A pattern in the amount and type of gene diversity in Meesia triquetra along a latitudinal gradient was predicted. The amount of fruiting in M. triquetra over the arctic-boreal gradient was not investigated quantitatively, but far fewer sporophytes were observed in high arctic sites than in subarctic and boreal sites both in the growth chamber during the culturing period, and in the field (unpubl. obs.).

In fact, the gene diversity of Meesia triquetra does decrease with latitude. Also, values of D in multidimensional space indicate that the boreal sites are farthest from the high arctic sites and the subarctic sites sit in an intermediate position.

The floristic age of the regions may have bearing on the amount of gene diversity in the region. The high arctic and boreal populations both underwent glaciation relatively recently compared to the subarctic region, thus the subarctic region is older than the other two regions. The oldest region would be expected to have the greatest genetic diversity first because the populations there would have the most time to develope mutations and second, because the yonger regions would have been colonized by only a few members of the old populations. Indeed the highest amount of inter-site gene diversity was found in the subarctic region. Packer and Vitt (1974) have suggested that a refugium existed during the Wisconsinan glaciation near Mountain Park, Alberta which is less than 100 km from the boreal sites used in this study. In which case, the boreal sites which have the highest intra-site gene diversity may have been colonized by very old populations which survived the Wisconsinan glaciation in the Mountan Park refugium.

The type of gene diversity was expected to vary with latitude if selective pressures vary with latitude, and electrophoretically detectable genetic variation is an indicator of total genetic variation. Changes in the type of gene diversity along the gradient were less clear than the changes in the amount of gene diversity over the gradient. The PCA excluding individual deme data (Fig. VI-2) shows a separation of the boreal sites from the sites of the other two regions. There is considerable overlap between the high arctic and subarctic sites, although the former are far more restricted in the principal component space. The PCA which included the data for the assayed demes (Fig. VI-5) shows separation of regions very clearly, but the arrangement of the regions is affected by the presence of the deme data, especially the boreal deme with the slow Mdh-3 allele. The genotypic character of the boreal sites differs substantially from sites of the two northern regions and there

appears to be some difference between the subarctic and the high arctic regions. Possibly the very restricted range of the high arctic sites is due to a high proportion of vegetative reproduction relative to sexual reproduction. The phenogram based on values of I between sites (Fig. VI-3) showed little evidence for variation with latitude; sites did not fall into clusters based on region.

Evidently, the amount of gene diversity in M. triquetra is related to latitude, possibly through historic events or through variation in the amount of sexual reproduction in populations along the gradient. Since the type of genetic variation in M. triquetra does not appear to follow a latitudinal gradient, I suggest that selective pressures along the arctic-boreal gradient may be less effective in generating genetic variation than random genetic drift.

Genotypic relationships between demes and their sites of origin.

The third objective of this study was to determine to what degree the gene diversity in a deme is representitive of the site as a whole, and to determine whether the relationship between the deme and its site of origin varies with latitude. If size of clones in a site is much larger than an individual deme (say the size of the site) I would expect that the deme would be a good predictor of the genetic structure of the site. Also if tclone size in the site was extremely small (for example, in a random arrangement of stems which are genetic individuals) I would expect the deme to be a good predictor of the genetic structure of the site. Alternatively, if the genetic heterogeneity was in a clumped pattern of clones close to the scale of the individual deme, I would expect the deme to be a poor predictor of the genetic structure of the site, in that the deme would only include a small number of clones relative to the total number of clones in the site as a whole.

In Meesia triquetra, gene diversity within a deme appears to be proportional to the amount of variation in the site as a whole. The genetic identity of demes of M. triquetra

and their sites of origin increases with latitude. Since we know that the gene diversity is relatively high in the boreal sites (Table VI-1), intermediate in the subarctic sites and low in the high arctic sites, we can conclude that the demes become better predictors with latitude because the sites become more genetically homogeneous at a scale larger than the deme (24 cm^2) from the boreal to the high arctic regions, in other words, clone size appears to increase with increasing latitude. Larger clones would be expected in areas where the amount of sexual reproduction is relatively low.

Conclusions

Meesia triquetra is one among many bryophytes with genetic diversities comparable to those of vascular plants and some animals. The existence of these genetically diverse species of mosses and liverworts contradicts the hypotheses which state that bryophytes have low gene diversity due to their dominant haploid state, short gene flow distances, and low incidence of sexual reproduction. Rather, bryophytes appear to possess a moderate amount of gene diversity indicating a moderate evolutionary potential; gene diversity being required for natural selection or genetic drift to take place. The amount of genetic variation in bryophytes is certainly as high as many vascular plant species which indicates that bryophytes may have the potential to evolve as rapidly as vascular plants. Indeed, it may be that bryophytes have not evolved simply because selective pressures are acting to stabilize their characters rather than to modify them, or alternatively, that bryophytes evolve in physiology rather than morphology as suggested by Wyatt et al. (1989b). The potential to evolve seems to be affected by environmental factors, such as those associated with changes in latitude, as indicated by the decrease in gene diversity in M. triquetra with latitude. It is not entirely clear why sexual reproduction is rare in the north relative to the south, but low temperatures, short growing seasons, low light intensity, and low nutrient availability in the arctic may play important roles.

Finally, the amount of genetic variation in Meesia triquetra appears to be controlled more by sexual reproduction and possibly historic events than random mutations. The amount of gene diversity in this moss decreases with latitude as does sexual reproduction, whereas I would expect mutation to be random rather than occurring in relationship to an environmental gradient, although there is evidence that mutation may be partially environmentally induced (Eckhardt -Schupp 1989; Lenski 1989; and Roth et al. 1989). Mutation as a source of genetic variation at the population level requires a great deal further investigation.

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VII. General Conclusions and Discussion

Meesia triquetra (Richt.) Aongstr. is a rich fen indicator species of high fidelity and a long-lived perennial of stable habitats. It occurs in alkaline fens with high pH (6.5 -7.5) and high calcium concentrations (30 - 60 $mg \cdot l^{-1}$), and with other bryophyte species common to rich fens such as Catoscopium nigritum (Hedw.) Brid., Scorpidum scorpioides (Hedw.) Limpr., and Tomenthypnum nitens (Hedw.) Schwaegr. The present day distribution of M. triquetra in North America ranges from northernmost Ellesmere Island in the Canadian Arctic south to California and Montana in the west, and Pennsylvania and Wisconsin in the east. Also, collections have been made from western Alaska east to Newfoundland. Quaternary subfossil records indicate that past populations of M. triquetra have occurred in a similar distribution to that of the present day, although the distribution appears to have extended slightly farther to the south at different periods in the last twenty thousand years.

Meesia triquetra was used as a representative species to explore the evolutionary potential in mosses. Variation in habitat, morphology, growth response, and genetics were investigated from several populations along an arctic-boreal gradient. Variation in a number of biological aspects along an environmental gradient indicates local adaptation, which in turn indicates a potential for evolution. The strength of the relationship between the gradient and the biology of the plant indicates the degree of evolutionary potential.

1. Habitat

The habitat section of this study is unsuccessful in clearly determining whether or not the surface water chemistry of the fens in which M. triquetra occurs varies with latitude. A far more rigorous study would be necessary to achieve that objective. A drought in the Yukon during the sampling season may have affected the water chemistry so that it is difficult to

determine whether the few differences detected among water samples taken from the three ecoclimatic regions are actual or merely a result of the particular season in which the study was done. It is also difficult to determine whether some of the high ion concentrations recorded were typical of M. triquetra habitats in the Yukon. However, some useful information was gleaned from this study. Many water quality variables do not vary significantly with latitude indicating that the aquatic habitat of M. triquetra does not change substantially from fen to fen along the arctic-boreal gradient, and also indicating that M. triquetra is fairly limited in its distribution by habitat availability, as has long been thought (Odgaard 1988 and Slack et al 1980). The pH range of waters analysed in this study is particularly narrow in range, most values falling between 6.6 and 8.0. The few water quality variables that do vary with latitude; dissolved phosphorus and and total phosphorus concentrations, turbidity, and pH, can be explained in part by changes in the environment surrounding the fens over the gradient. Again, whether the variation in these characters is due in part to changes in habitat preference of M. triquetra is not clear.

2. Morphology.

Morphological variation due to either phenotypic plasticity or genetic variation can lead to the expansion of species distributions, thereby exposing plants to new selective pressures. These selective pressures can, in turn, lead to further variation or even speciation (Longton 1979; and Stearns 1989), thus morphological variation can be used as an indicator of evolutionary potential. Eleven morphological characters were measured in each of three plants from 109 herbarium specimes. The specimens were equally distributed in three ecoclimatic regions: High Arctic, Low Arctic, and Boreal Forest. Nine of the eleven morphological characters vary significantly with latitude, although the amount of variation accounted for by the latitudinal gradient is low; from 1% in cell width and up to only to 16% in leaf shape. Principal component site scores for both principal components 1 and 2

also vary significantly with latitude and have low r^2 values. Discriminant analysis indicates that the morphological variation in M. triquetra is substantial enough to allow for discrimination among specimens from different ecoclimatic regions based on latitude by morphology alone. Nested multivariate analysis of variance indicates that there are significant differences among specimens from the three ecoclimatic regions and among specimens from different sites. At the plant level of replication, the morphology of specimens from the three ecoclimatic regions are significantly different from each other, whereas at the leaf and cell levels of replication, specimens from the Boreal and Low Arctic ecoclimatic regions are indistinguishable but they are significantly different from those of the High Arctic region. Possibly the presence of trees surrounding the fens in which M. triquetra grows affects the morphology of the moss through increased nutrient input and protection from the wind and possibly from the sun. At the leaf and cell levels of replication significant differences were detected among plants, although the majority of the variation detected was within plants.

Generally, the morphological trends in Meesia triquetra parallel those of vascular plants, in that annual growth is diminished in the north relative to the south. Annual growth increments lengths and weights, and leaf lengths decrease with latitude. The vascular flora of the arctic is well known to be small in stature; this is controlled both genetically through selective pressures such as wind and its associated effects, and phenotypically through low temperatures and nutrient availability (Bliss 1962; Chapin 1983; Savile 1972; and Warren Wilson 1966). The difference in leaf shape along the arctic-boreal gradient results in plants with a more compact growth from in the arctic compared to those of the south. Compact growth-forms are characteristic of bryophytes in water stressed habitats (Birse 1957; and Gimmingham and Birse 1957) and of the arctic flora in general (Savile 1972). Compact growth-forms are thought to decrease the risk of water loss and frost damage.

In conclusion, the morphology of Meesia triquetra varies over an arctic-boreal gradient, and although the relationship between morphology and latitude is significant, it is not particularly strong, which indicates that M. triquetra is capable of adapting to local environments to a certain extent, thus this moss may possess a moderate potential to evolve. The large amount of morphological variation not accounted for by the latitudinal gradient may be due to genetic differences in the moss or to the effects of meso- or microenvironmental gradients not examined in this study.

3. Growth

No significant difference was found in the annual growth increments lengths of Meesia triquetra measured in a high arctic fen and a boreal fen grrowing under natureal conditions. However, the boreal population grew significantly more within a seven week growing period than the arctic population under simulated boreal conditions. The difference in growth rate in a controlled environment suggests that the physiology controlling growth in the arctic population was unable to function efficiently under boreal conditions. Thus the arctic population appears to be locally adapted to its environment. The ability to adapt to local environments indicates the ability of the species to diverge and evolve.

Meesia triquetra shows no plastic response in growth rate to the aquatic environment in which it grows. Stems from the arctic and the boreal populations grew the same rate whether they were grown in water from the arctic or the boreal fen despite the higher concentrations of sodium, potassium, calcium, magnesium, and phosphorus and lower nitrogen concentrations in the boreal fen water relative to the arctic fen water. Also the pH of the of the boreal water is close to the mean pH for fens in which M. triquetra occurs at 7.6, whereas the arctic water has a pH at the upper extreme of the moss' natural habitat at 8.1 (chapter II). Furthermore, no difference in growth was detected between plants grown with a nitrogen treatment and those grown in natural water.

Nitrogen fertilization of the levels used in this experiment appear to have no effect on the growth of Meesia triquetra. This result was surprising because many Sphagnum species fertilized at this level showed either enhanced or diminished growth (Austin and Weider 1986; Rudolf and Voigt 1986; and Press et al. 1986). Acid rain with relatively high concentrations of nitric acid may pose different threats to mosses like Sphagnum that are sensitive to nitrogen than to mosses like M. triquetra. Moreover, nitrogen appears not to be a limiting factor in the growth of M. triquetra.

In conclusion, growth rates in the two populations of Meesia triquetra investigated in this study are significantly different, and since variation due to natural selection or random genetic drift is indicative of evolutionary potential, I suggest that this moss, and possibly others, are well equipped with a high potential to evolve.

4. Genetics

The genetic diversity detected in Meesia triquetra is comparable to those found in other mosses (de Vries et al. 1983 and 1989; Wyatt et al. 1989; and Yamazaki 1981). Meesia triquetra has a genetic diversity much higher than some selfing vascular plants (Levin 1978 and Nevo et al. 1979) and even the out crossing Gaura longiflora (Gottlieb and Pilz 1976), although not as high as Picea abies (Lundkvist 1979).

The sites in this study are more similar to one another than are populations of other moss species reported (Daniels 1982; de Vries et al 1983 and 1989; and Wyatt et al. 1989) which indicates that the variation in M. triquetra is relatively consistant throughout its range in terms genetic diversity. Other mosses show less similarity among populations than among populations of many vascular plant species (Crawford and Smith 1982; Lundkvist 1979; Soltis 1981; and Yeh and O'Malley 1980) and even among populations of some animal species (Crouau-Roy 1989a, 1989b; and Kovacic and Guttman 1979). High

genetic identities among sites many indicate that either the rate of gene flow is high among populations.

Although Meesia triquetra has low genetic variability, both in genetic diversity and among sites, relative to other moss species, this moss is comparable in both these indices to many vascular plant and animal species. Evidently, if M. triquetra and other mosses are evolving slowly compared to other organisms, it is not because they have depauperate genotypes.

The amount of fruiting in M. triquetra along the arctic-boreal gradient was not measured quantitatively, but far fewer sporophytes were observed in high arctic sites than in subarctic or boreal sites, therefore I hypothesised that the genetic diversity in M. triquetra would be lower in the north than in the south. Also, I have suggested that the selective pressures acting on M. triquetra would change over the latitudinal gradient resulting in a gradual change in electrophoretically detectable variation over the gradient, assuming that electrophoretically detectable variation is representitive of all variation in the plant.

The amount of genetic diversity decreased with latitude as was expected. Also, genetic distances in multidimentional space indicate that the boreal sites are farthest from the high arctic sites, and the subarctic sites sit in an intermediate position. Changes in the type of genetic diversity with the gradient were less clear. Principal components analysis indicated that the boreal sites are separated from sites in the other two regions, but the subarctic and high arctic sites are overlapping in their genetic structure. Phenograms based on genetic identity show no pattern of grouping of sites from the three ecoclimatic regions. Evidently, the amount of genetic diversity in M. triquetra is related to latitude, but the genetic structures of the sites are not. I suggest that selective pressures along the latitudinal gradient are less effective in generating genetic diversity than random genetic drift.

In Meesia triquetra, genetic diversity within a deme appears to be proportional to the amount of variation in the site as a whole. The genetic distances between demes of M. triquetra and their sites of origin decreases with increasing latitude. Since genetic diversity is high in the boreal sites, low in the high arctic sites, and intermediate in the subarctic sites, it can be concluded that demes become better predictors with latitude because the sites become more genetically homogenous at a scale larger than the deme along the latitudinal gradient. In other words, clone size increases with increasing latitude.

General conclusions

Variation along a latitudinal gradient indicates local adaptation and a potential for evolution. The morphology of Meesia triquetra varies significantly with latitude and the variation is substantial enough to allow for discrimination of specimens from three ecoclimatic regions based on latitude by morphology alone. Growth rates in M.triquetra decrease with latitude and the difference in growth rates between an arctic and boreal population of this moss appears to be genetically controlled with very little affect from the aquatic environment in which the moss lives. Such a genetic difference may be interpreted as adaptation to different environments since rapid growth could reduce fitness in the harsh arctic environment. Genetic diversity in M. triquetra is comparable to genetic diversity in many plant and animal species. Therefore, if mosses like M. triquetra are evolving at a slower rate than vascular plants or animals, it is not because they possess a depauperate genotype.

In conclusion, Meesia triquetra demonstrates an active potential to evolve based on the variation it exhibits in morphology, growth rate, and genetics. The broad distribution of this moss indicates its ecological success throughout a range of macroclimates. Ecological success need not be at the expense of genetic diversity or evolutionary potential as was suggested by Crum (1972). Indeed, if a species is ecologically successful it is because it has evolved to that state through natural selection. Although evolution implies

change, natural selection can act to stabilize traits rather than change them. I suggest that if M. triquetra evolves slowly, it is because it is well suited to its environment, not because it possesses a low potential for evolution.

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Appendix 1

Surface water chemistry of 15 fens in which Meesia triquetra occurs. (EL = Ellesmere sites, YT = Yukon sites, and AB = Alberta sites.)

Site	Total Phosphorus $\mu g \cdot L^{-1}$	Total Dissolved Phosphorus $\mu g \cdot L^{-1}$	Nitrate $\mu g \cdot L^{-1}$	Ammonium $\mu g \cdot L^{-1}$	Sodium $mg \cdot L^{-1}$	Potassium $mg \cdot L^{-1}$
EL1	16.8	2.7	5.2	7.2	2.69	0.69
EL2	1.3	1.6	6.8	3.1	0.32	0.12
EL3	15.2				2.23	0.21
EL4	73.6	3.5	5.8	3.5	3.09	0.57
EL5	10.3	3.3	4.2	5.4	2.70	0.16
YT1	322.7	8.6	26.3	66.5	0.48	0.67
YT2	129.8	9.0	7.0	45.0	1.81	1.49
YT3	83.8	7.4	0.6	30.1	0.76	0.41
YT4	201.1	7.8	3.5	17.4	4.26	0.63
YT5	74.6	11.2	5.8	3.2	2.11	1.19
AB1	32.8	8.8	0.0	4.8	1.51	0.92
AB2	47.8	7.7	1.2	0.0	1.27	0.21
AB3	78.8	8.2	1.1	19.5	0.45	1.02
AB4	39.7	10.8	3.4	49.9	0.15	0.94
AB5	29.6	8.1	2.9	0.1	3.43	0.49

Site	Calcium $mg \cdot L^{-1}$	Magnesium $mg \cdot L^{-1}$	Sulphate $mg \cdot L^{-1}$	Chloride $mg \cdot L^{-1}$	pH	Alkalinity $meq \cdot L^{-1}$
1	60.46	12.08	1.9	5.5	7.60	233.9
2	37.36	6.44	2.4	0.9	8.06	154.2
3	28.86	9.77	1.9	8.5	7.82	134.8
4	27.15	14.55	3.7	8.5	7.50	148.3
5	38.46	8.72			7.08	170.2
YT1	62.94	7.74	10.7	0.8	7.70	226.8
YT2	79.94	26.92	63.0	22.5	7.27	329.6
YT3	117.03	34.42	447.5	0.9	7.41	171.3
YT4	32.42	11.16	17.1	5.6	7.20	158.0
YT5	45.28	18.11	19.5	1.8	7.41	194.2
AB1	40.16	7.62	0.0	3.3	7.56	173.9
AB2	12.65	1.85	0.0	0.0	7.26	47.5
AB3	22.37	6.93	0.0	0.5	6.74	84.1
AB4	34.30	9.00	0.0	0.1	7.31	122.6
AB5	40.40	10.24	0.0	0.3	7.01	151.0

Site	Conductivity µS	Turbidity NTU	Colour mg Pt $\cdot L^{-1}$
1	480	20.0	10.0
2	305	7.5	0.9
3	300	7.5	6.9
4	330	8.3	10.5
5	370		
YT1	410	25.0	11.0
YT2	900	30.0	0.3
YT3	1035	40.0	28.0
YT4	220	10.0	12.0
YT5	450	10.0	7.5
AB1	350	60.0	10.0
AB2	100	20.0	21.0
AB3	190	50.0	7.7
AB4	265	50.0	9.8
AB5	330	50.0	10.0

Appendix 2-A

Morphological character measurements in Meesia triquetra - Plants and site locations. Where: A = site number, B = plant number, C = latitude score, D= longitude score, E = annual growth increment length (mm), F = number of leaf whorls per annual growth increment, G= number of leaf whorls per cm growth, H = annual growth increment dry weight (g), I = dry weight per mm growth (g), and J = ecoclimatic region (1 = High Arctic, 2 = Low Arctic, 3 = Boreal).

A	B	C	D	E	F	G	H	I	J
1	1	5352	11660	6.9	6	9	0.54	0.08	3
1	2	5352	11660	9.8	7	8	0.90	0.09	3
1	3	5352	11660	10.9	16	14	0.76	0.07	3
2	1	5433	12592	12.0	8	7	0.76	0.06	3
2	2	5433	12592	9.3	5	6	0.51	0.05	3
2	3	5433	12592	9.9	7	7	0.52	0.05	3
3	1	5935	6400	12.9	11	7	1.04	0.08	2
3	2	5935	6400	12.3	11	10	1.63	0.13	2
3	3	5935	6400	13.7	9	6	0.66	0.05	2
4	1	5607	12813	20.6	11	6	0.73	0.04	3
4	2	5607	12813	12.2	7	5	0.55	0.05	3
4	3	5607	12813	11.1	7	6	0.57	0.05	3
5	1	5823	12948	13.9	15	10	0.70	0.05	2
5	2	5823	12948	11.5	11	8	0.78	0.07	2
5	3	5823	12948	10.4	11	10	0.46	0.04	2
6	1	6812	16592	6.5	7	10	0.87	0.13	2
6	2	6812	16592	8.7	10	11	0.43	0.05	2
6	3	6812	16592	9.2	7	9	0.52	0.06	2
7	1	7150	15700	6.5	7	14	0.31	0.05	2
7	2	7150	15700	5.8	8	12	0.43	0.07	2
7	3	7150	15700	8.7	8	10	0.36	0.04	2
8	1	6867	14100	8.3	12	14	0.70	0.08	2
8	2	6867	14100	5.7	7	16	0.28	0.05	2
8	3	6867	14100	9.5	11	12	0.31	0.03	2
9	1	5248	11605	8.6	21	23	0.65	0.08	3
9	2	5248	11605	7.5	15	22	0.47	0.06	3
9	3	5248	11605	6.1	15	23	0.32	0.05	3
10	1	7575	8002	9.4	7	7	0.62	0.07	1
10	2	7575	8002	8.9	8	9	0.61	0.07	1
10	3	7575	8002	7.7	6	8	0.45	0.06	1
11	1	6535	13833	11.7	15	10	0.93	0.08	3
11	2	6535	13833	13.6	19	12	1.23	0.09	3
11	3	6535	13833	12.8	18	12	1.28	0.10	3
12	1	5712	11148	13.1	6	5	0.44	0.03	3
12	2	5712	11148	15.3	10	7	0.77	0.05	3

A	B	C	D	E	F	G	H	I	J
12	3	5712	11148	7.5	7	7	0.35	0.05	3
13	1	5707	11150	5.3	14	23	0.25	0.05	3
13	2	5707	11150	8.2	9	12	0.79	0.10	3
13	3	5707	11150	3.8	7	15	0.26	0.07	3
14	1	5702	11150	7.3	5	8	0.13	0.02	3
14	2	5702	11150	11.0	10	9	0.24	0.02	3
14	3	5702	11150	11.3	10	10	0.29	0.03	3
15	1	6867	14100	4.6	5	16	0.31	0.07	3
15	2	6867	14100	4.5	5	16	0.39	0.09	3
15	3	6867	14100	4.2	5	19	0.41	0.10	3
16	1	5712	11148	13.5	10	8	0.74	0.05	3
16	2	5712	11148	10.7	11	9	0.67	0.06	3
16	3	5712	11148	14.0	10	6	0.88	0.06	3
17	1	5705	11145	7.7	7	12	0.62	0.08	3
17	2	5705	11145	9.8	7	7	0.58	0.06	3
17	3	5705	11145	6.9	6	10	0.34	0.05	3
18	1	5412	12222	13.0	9	7	1.64	0.13	3
18	2	5412	12222	12.1	17	12	2.41	0.20	3
18	3	5412	12222	7.9	12	14	0.76	0.10	3
19	1	7572	9842	5.6	5	8	0.36	0.06	1
19	2	7572	9842	10.2	6	6	0.56	0.05	1
19	3	7572	9842	10.0	6	8	0.35	0.04	1
20	1	5452	12268	9.7	9	8	1.00	0.10	3
20	2	5452	12268	9.7	10	9	0.74	0.08	3
20	3	5452	12268	7.8	7	10	0.86	0.11	3
21	1	5205	11508	6.5	4	7	0.20	0.03	3
21	2	5205	11508	10.3	7	7	0.57	0.06	3
21	3	5205	11508	16.7	13	8	1.35	0.08	3
22	1	5607	12913	12.4	7	6	0.46	0.04	3
22	2	5607	12913	10.0	5	5	0.34	0.03	3
22	3	5607	12913	10.2	7	6	0.65	0.06	3
23	1	5823	12948	11.0	7	5	0.60	0.05	3
23	2	5823	12948	9.6	8	9	0.56	0.06	3
23	3	5823	12948	7.1	5	7	0.49	0.07	3
24	1	6257	12852	7.2	8	11	0.37	0.05	3
24	2	6257	12852	5.9	6	11	0.31	0.05	3
24	3	6257	12852	5.2	7	12	0.55	0.11	3
25	1	6257	12863	8.0	8	12	0.35	0.04	3
25	2	6257	12863	9.1	8	11	0.54	0.06	3
25	3	6257	12863	5.6	8	14	0.33	0.06	3
26	1	5242	12117	12.8	10	9	0.97	0.08	3
26	2	5242	12117	9.4	9	9	0.52	0.06	3
26	3	5242	12117	10.0	8	8	0.70	0.07	3
27	1	7613	10812	5.0	4	9	0.34	0.07	1
27	2	7613	10812	5.0	4	11	0.26	0.05	1
27	3	7613	10812	3.8	3	11	0.22	0.06	1
28	1	6133	12142	4.0	4	8	0.27	0.07	3
28	2	6133	12142	4.2	5	10	0.20	0.05	3
28	3	6133	12142	3.0	5	14	0.11	0.04	3
29	1	5270	11683	14.6	22	11	0.60	0.04	3
29	2	5270	11683	19.7	25	11	1.66	0.08	3
29	3	5270	11683	15.7	21	13	1.85	0.12	3
30	1	6143	12815	6.4	7	9	0.34	0.05	3
30	2	6143	12825	6.0	6	11	0.25	0.04	3
30	3	6143	12825	5.7	7	12	0.38	0.07	3
31	1	5447	12275	13.6	10	7	0.64	0.05	3
31	2	5447	12275	14.0	11	8	0.97	0.07	3
31	3	5447	12275	16.0	14	8	0.45	0.03	3
32	1	6848	15405	11.9	8	6	0.78	0.07	2
32	2	6848	15405	11.1	8	7	1.30	0.12	2

A	B	C	D	E	F	G	H	I	J
32	3	6848	15405	14.6	11	7	1.41	0.10	2
33	1	6788	15508	7.2	9	15	0.74	0.10	2
33	2	6788	15508	5.6	8	14	0.33	0.06	2
33	3	6788	15508	6.5	9	15	0.89	0.14	2
34	1	5270	11683	8.1	6	8	0.47	0.06	3
34	2	5270	11683	10.8	9	9	0.64	0.06	3
34	3	5270	11683	10.4	9	7	0.73	0.07	3
35	1	5137	11617	8.0	15	17	0.73	0.09	3
35	2	5137	11617	8.9	16	16	0.78	0.09	3
35	3	5137	11617	7.0	14	16	0.65	0.09	3
36	1	6257	12853	8.0	7	9	1.04	0.13	3
36	2	6257	12853	13.1	9	7	1.07	0.08	3
36	3	6257	12853	8.4	7	8	0.91	0.11	3
37	1	7572	9842	3.7	4	12	0.41	0.11	1
37	2	7572	9842	5.0	5	12	0.60	0.12	1
37	3	7572	9842	3.5	4	12	0.44	0.13	1
38	1	6685	9542	12.4	14	11	0.89	0.07	2
38	2	6685	9542	10.2	10	11	0.31	0.03	2
38	3	6685	9542	8.2	9	12			2
39	1	5675	11197	6.3	9	12	0.26	0.04	3
39	2	5675	11197	7.9	13	16	0.42	0.05	3
39	3	5675	11197	5.9	10	16	0.16	0.03	3
40	1	6980	15538	6.5	7	11	0.45	0.07	2
40	2	6980	15538	9.0	11	11	0.74	0.08	2
40	3	6980	15538	10.8	11	10	1.06	0.10	2
41	1	7047	9383	2.9	7	19	0.26	0.09	1
41	2	7047	9383	3.5	5	15	0.42	0.12	1
41	3	7047	9383	4.3	5	16	0.35	0.08	1
42	1	6608	11803	11.8	12	10	1.32	0.11	2
42	2	6608	11803	11.2	12	8	1.25	0.11	2
42	3	6608	11803	11.0	10	9	0.84	0.08	2
43	1	6988	14230	3.0	3	13	0.14	0.05	2
43	2	6988	14230	3.7	5	12	0.30	0.08	2
43	3	6988	14230	3.0	4	14	0.24	0.08	2
44	1	5350	11400	10.2	13	13	0.74	0.07	3
44	2	5350	11400	9.1	10	11	0.41	0.05	3
44	3	5350	11400	13.6	17	12	0.74	0.05	3
45	1	6770	13747	7.0	7	12	0.31	0.04	2
45	2	6770	13747	5.2	10	13	0.43	0.08	2
45	3	6770	13747	6.0	9	12	0.55	0.09	2
46	1	5248	11605	8.7	12	14	0.31	0.04	3
46	2	5248	11605	7.4	11	14	0.49	0.07	3
46	3	5248	11605	6.1	9	16	0.35	0.06	3
47	1	5215	11487	13.8	18	11	1.15	0.08	3
47	2	5215	11487	12.2	14	11	0.51	0.04	3
47	3	5215	11487	13.1	16	11	0.43	0.03	3
48	1	7000	15000	4.8	5	11	0.43	0.09	2
48	2	7000	15000	6.9	10	15	0.50	0.07	2
48	3	7000	15000	4.8	7	14	0.47	0.10	2
49	1	7567	8467	7.1	6	10	0.60	0.08	1
49	2	7567	8467	8.6	5	6	0.81	0.09	1
49	3	7567	8467	9.3	5	6	0.93	0.10	1
50	1	4820	8675	3.0	5	18	0.18	0.06	3
50	2	4820	8675	4.3	4	12	0.23	0.05	3
50	3	4820	8675	5.9	7	14	0.29	0.05	3
51	1	7567	8467	11.4	8	7	0.68	0.06	1
51	2	7567	8467	8.4	5	5	0.35	0.04	1
51	3	7567	8467	8.0	7	7	0.61	0.08	1
52	1	6937	15213	5.1	5	10	0.21	0.04	2
52	2	6937	15213	5.4	5	11	0.19	0.04	2

A	B	C	D	E	F	G	H	I	J
52	3	6937	15213	4.5	5	12	0.27	0.06	2
53	1	5452	12268	10.6	10	10	0.82	0.08	3
53	2	5452	12268	5.1	5	9	0.42	0.08	3
53	3	5452	12268	10.5	8	8	0.64	0.06	3
54	1	5505	12303	22.7	20	8	2.27	0.10	3
54	2	5505	12303	28.6	21	6	2.16	0.08	3
54	3	5505	12303	22.4	17	5	1.75	0.08	3
56	1	7567	8467	3.0	5	18	0.57	0.19	1
56	2	7567	8467	5.9	9	20	0.84	0.14	1
56	3	7567	8467	4.9	9	18	0.69	0.14	1
57	1	7580	8370	8.4	7	8	0.91	0.11	1
57	2	7580	8370	10.2	7	6	0.96	0.09	1
57	3	7580	8370	11.1	7	7	0.98	0.09	1
58	1	7526	9840	5.0	8	15	0.44	0.09	1
58	2	7526	9840	5.0	9	15	0.36	0.07	1
58	3	7526	9840	5.0	7	13	0.45	0.09	1
59	1	7567	8467	6.9	10	14	0.99	0.14	1
59	2	7567	8467	5.5	7	11	0.41	0.07	1
59	3	7567	8467	5.8	6	12	0.56	0.10	1
60	1	7575	8402	4.6	4	11	0.31	0.07	1
60	2	7575	8402	2.8	3	16	0.18	0.06	1
60	3	7575	8402	5.7	4	9	0.30	0.05	1
61	1	7567	8467	4.2	3	10	0.26	0.06	1
61	2	7567	8467	4.9	5	10	0.37	0.08	1
61	3	7567	8467	5.3	5	10	0.72	0.14	1
62	1	7133	15700	6.6	9	15	0.42	0.06	2
62	2	7133	15700	5.9	7	13	0.38	0.06	2
62	3	7133	15700	3.5	6	22	0.24	0.07	2
63	1	7567	8467	14.6	11	6	1.46	0.10	1
63	2	7567	8467	14.5	11	6	1.15	0.08	1
63	3	7567	8467	15.1	10	7	1.49	0.10	1
64	1	7567	8467	11.9	9	7	1.08	0.09	1
64	2	7567	8467	14.2	10	7	1.09	0.08	1
64	3	7567	8467	8.7	7	9	0.82	0.09	1
65	1	4750	13000	8.0	10	13	1.09	0.14	3
65	2	4750	13000	10.4	12	12	1.00	0.10	3
65	3	4750	13000	4.6	8	15	0.45	0.10	3
66	1	8217	3100	8.1	7	10	0.94	0.12	1
66	2	8217	3100	6.4	7	10	0.63	0.10	1
66	3	8217	3100	5.6	5	9	0.30	0.05	1
67	1	6735	15690	18.5	17	8	1.74	0.09	2
67	2	6735	15690	21.9	15	5	1.59	0.07	2
67	3	6735	15690	20.6	15	9	1.62	0.08	2
68	1	6788	15508	6.0	8	15	0.51	0.09	2
68	2	6788	15508	5.8	8	13	0.53	0.09	2
68	3	6788	15508	7.5	7	11	0.50	0.07	2
69	1	7450	8500	5.4	8	13	0.33	0.06	1
69	2	7450	8500	7.3	8	10	0.27	0.04	1
69	3	7450	8500	7.9	7	10	0.35	0.04	1
70	1	6633	6550	8.2	9	11	0.72	0.09	1
70	2	6633	6550	11.0	11	10	1.01	0.09	1
70	3	6633	6550	12.1	11	9	0.91	0.08	1
71	1	6952	13382	30.4	21	6	1.71	0.06	2
71	2	6952	13382	24.4	14	5	0.83	0.03	2
71	3	6952	13382	30.0	19	6	1.49	0.05	2
72	1	6983	14867	7.0	9	18	0.81	0.12	2
72	2	6983	14867	6.2	9	15	0.67	0.11	2
72	3	6983	14867	1.9	4	23	0.16	0.08	2
73	1	6812	16592	10.0	9	11	0.81	0.08	2
73	2	6812	16592	12.0	12	9	1.16	0.10	2

A	B	C	D	E	F	G	H	I	J
73	3	6812	16592	8.5	12	14	0.97	0.11	2
74	1	6872	15650	17.7	15	6	1.05	0.06	2
74	2	6872	15650	14.8	12	6	1.03	0.07	2
74	3	6872	15650	16.0	14	7	1.14	0.07	2
75	1	6872	15650	6.5	10	15	0.52	0.08	2
75	2	6872	15650	9.1	11	11	0.53	0.06	2
75	3	6872	15650	6.3	8	14	0.41	0.07	2
76	1	7000	16100	3.4	8	17	0.15	0.04	2
76	2	7000	16100	3.9	9	16	0.18	0.05	2
76	3	7000	16100	3.9	8	17	0.36	0.09	2
77	1	6980	15538	7.6	9	15	0.37	0.05	2
77	2	6980	15538	7.6	12	14	0.62	0.08	2
77	3	6980	15538	7.7	12	14	1.01	0.13	2
78	1	6878	16000	2.9	7	16	0.26	0.09	2
78	2	6878	16000	2.9	5	19	0.32	0.11	2
78	3	6878	16000	2.4	4	20	0.20	0.08	2
79	1	7095	15745	14.1	11	9	0.86	0.06	2
79	2	7095	15745	9.3	6	6	0.76	0.08	2
79	3	7095	15745	8.8	9	10	0.54	0.06	2
80	1	8198	7047	3.8	7	17	0.27	0.07	1
80	2	8198	7047	3.8	5	18	0.20	0.05	1
80	3	8198	7047	4.3	6	12	0.25	0.06	1
81	1	7467	9500	2.0	4	16	0.10	0.05	1
81	2	7467	9500	3.1	4	16	0.25	0.08	1
81	3	7467	9500	3.3	5	16	0.36	0.11	1
82	1	7942	9075	4.5	6	9	0.18	0.04	1
82	2	7942	9075	4.7	4	10	0.31	0.07	1
82	3	7942	9075	5.7	5	11	0.58	0.10	1
83	1	7280	7885	7.8	6	7	0.43	0.06	1
83	2	7280	7885	8.0	7	9	0.56	0.07	1
83	3	7280	7885	8.4	9	11	0.53	0.06	1
84	1	7280	7885	5.1	6	10	0.33	0.06	1
84	2	7280	7885	5.9	6	14	0.35	0.06	1
84	3	7280	7885	4.8	6	12	0.44	0.09	1
85	1	7450	8500	14.0	9	6	0.79	0.06	1
85	2	7450	8500	14.4	7	5	0.62	0.04	1
85	3	7450	8500	12.8	7	5	0.53	0.04	1
86	1	6633	6550	9.5	10	11	0.37	0.04	1
86	2	6633	6550	9.1	10	11	0.26	0.03	1
86	3	6633	6550	8.0	7	9	0.37	0.05	1
87	1	8142	7692	8.1	6	8	0.61	0.08	1
87	2	8142	7692	9.5	6	7	0.65	0.07	1
87	3	8142	7692	9.0	6	8	0.88	0.10	1
88	1	7923	8617	4.5	9	14	0.57	0.13	1
88	2	7923	8617	5.3	7	11	0.60	0.11	1
88	3	7923	8617	5.3	7	14	0.58	0.11	1
89	1	6938	12530	9.5	11	11	0.71	0.07	2
89	2	6938	12530	11.0	9	7	0.83	0.08	2
89	3	6938	12530	13.5	10	6	0.87	0.06	2
90	1	7015	12797	8.1	10	17	0.95	0.12	2
90	2	7015	12797	7.4	13	17	0.68	0.09	2
90	3	7015	12797	5.8	10	19	0.88	0.15	2
91	1	7572	9842	6.9	5	10	0.51	0.07	1
91	2	7572	9842	10.4	8	7	0.65	0.06	1
91	3	7572	9842	10.9	8	6	0.70	0.06	1
92	1	7198	12520	11.9	12	7	0.57	0.05	1
92	2	7198	12520	10.0	12	12	0.85	0.09	1
92	3	7198	12520	10.0	13	13	0.90	0.09	1
93	1	7227	12350	5.5	6	14	0.45	0.08	1
93	2	7227	12350	3.2	6	16	0.35	0.11	1

A	B	C	D	E	F	G	H	I	J
93	3	7227	12350	4.8	5	18	0.48	0.10	1
94	1	7275	11850	4.1	5	11	0.48	0.12	1
94	2	7275	11850	3.8	6	13	0.63	0.17	1
94	3	7275	11850	2.4	4	13	0.16	0.07	1
95	1	7567	8467	8.0	7	10	1.02	0.13	1
95	2	7567	8467	6.9	6	11	0.68	0.10	1
95	3	7567	8467	8.6	8	10	0.88	0.10	1
96	1	7567	8467	7.7	8	10	0.96	0.12	1
96	2	7567	8467	7.6	7	11	0.84	0.11	1
96	3	7567	8467	7.8	7	9	0.75	0.10	1
97	1	7572	9842	5.3	6	11	0.65	0.12	1
97	2	7572	9842	4.8	7	16	0.74	0.15	1
97	3	7572	9842	4.0	6	13	0.50	0.13	1
98	1	6375	6853	4.4	5	14	0.96	0.22	1
98	2	6375	6853	3.1	5	17	0.47	0.15	1
98	3	6375	6853	4.3	6	15	0.67	0.16	1
99	1	6778	11550	5.4	7	12	0.67	0.12	2
99	2	6778	11550	5.7	7	11	0.83	0.15	2
99	3	6778	11550	5.8	6	11	0.76	0.13	2
100	1	6565	8880	10.0	9	9	0.81	0.08	2
100	2	6565	8880	16.0	12	9	1.28	0.08	2
100	3	6565	8880	10.0	8	8	0.58	0.06	2
101	1	6983	7067	16.6	8	6	0.73	0.04	1
101	2	6983	7067	15.6	9	7	0.71	0.05	1
101	3	6983	7067	15.8	9	6	0.76	0.05	1
102	1	5908	6392	17.8	13	8	1.46	0.08	2
102	2	5908	6392	17.7	12	8	1.78	0.10	2
102	3	5908	6392	16.1	12	8	0.69	0.04	2
103	1	5877	9417	8.4	11	13	1.13	0.13	2
103	2	5877	9417	8.5	13	16	1.09	0.13	2
103	3	5877	9417	9.1	10	13	0.89	0.10	2
104	1	7047	15742	5.5	9	16	0.81	0.15	2
104	2	7047	15742	3.2	6	19	0.29	0.09	2
104	3	7047	15742	7.4	11	14	0.67	0.09	2
105	1	7025	14867	2.5	5	22	0.28	0.11	2
105	2	7025	14867	2.5	4	20	0.24	0.10	2
105	3	7025	14867	1.8	4	24	0.19	0.11	2
106	1	6850	14942	9.7	10	11	1.21	0.12	2
106	2	6850	14942	8.8	10	11	0.95	0.11	2
106	3	6850	14942	7.4	10	11	0.78	0.11	2
107	1	6840	15485	3.1	9	23	0.41	0.13	2
107	2	6840	15485	3.0	8	21	0.33	0.11	2
107	3	6840	15485	4.2	11	24	0.42	0.10	2
108	1	6888	16117	2.4	7	20	0.35	0.15	2
108	2	6888	16117	2.3	6	22	0.19	0.08	2
108	3	6888	16117	2.2	6	18	0.26	0.12	2
109	1	7065	15692	8.9	13	16	1.18	0.13	2
109	2	7065	15692	8.0	12	14	0.72	0.09	2
109	3	7065	15692	12.4	13	12	1.17	0.09	2
110	1	6938	15217	3.2	4	12	0.21	0.07	2
110	2	6938	15217	2.8	4	12	0.25	0.09	2
110	3	6938	15217	2.7	5	12	0.24	0.09	2

Appendix 2-B

Morphological character measurements in Meesia triquetra - Leaves.

Where: A = site number, B = leaf number, C = leaf length (μm), D = length from leaf apex to leaf shoulder along the costa (μm), E = half leaf width, F = $\overline{D/E}$ = leaf shape.

A	B	C	D	E	F
1	1	2380.0	1815.0	530.0	3.4
1	2	2255.0	1630.0	557.5	2.9
1	3	2207.5	1695.0	535.0	3.2
1	4	1825.0	1215.0	315.0	3.9
1	5	2337.5	1817.5	412.5	4.4
1	6	2317.5	1847.5	417.5	4.4
1	7	2300.0	1640.0	617.5	2.7
1	8	1892.5	1307.5	500.0	2.6
1	9	2002.5	1430.0	565.0	2.5
2	1	2287.5	1645.0	482.5	3.4
2	2	2367.5	1565.0	590.0	2.7
2	3	2360.0	1705.0	670.0	2.5
2	4	2252.5	1620.0	530.0	3.1
2	5	2350.0	1605.0	540.0	3.0
2	6	2317.5	1672.5	580.0	2.9
2	7	1857.5	1225.0	567.5	2.2
2	8	1867.5	1215.0	360.0	3.4
2	9	1875.0	1320.0	445.0	3.0
3	1	2192.5	1470.0	472.5	3.1
3	2	2425.0	1700.0	592.5	2.9
3	3	2357.5	1607.5	545.0	2.9
3	4	2225.0	1630.0	560.0	2.9
3	5	2335.0	1835.0	605.0	3.0
3	6	2577.5	1790.0	387.5	4.6
3	7	2260.0	1592.5	445.0	3.6
3	8	2240.0	1555.0	352.5	4.4
3	9	1942.5	1470.0	427.5	3.4
4	1	2097.5	1217.5	487.5	2.5
4	2	1875.0	1357.5	540.0	2.5
4	3	2082.5	1340.0	515.0	2.6
4	4	2085.0	1367.5	580.0	2.4
4	5	2205.0	1532.0	557.5	2.7
4	6	2065.0	1300.0	575.0	2.3
4	7	2457.5	1845.0	475.0	3.9
4	8	2490.0	1770.0	522.5	3.4
4	9	2357.5	1737.5	645.0	2.7
5	1	1397.5	955.0	400.0	2.4
5	2	1862.5	1425.0	507.5	2.8
5	3	1865.0	1282.0	465.0	2.8
5	4	2200.0	1555.0	530.0	2.9
5	5	1815.0	1142.5	392.5	2.9
5	6	2157.5	1412.5	590.0	2.4
5	7	1757.5	1165.0	477.0	2.4
5	8	1527.5	1182.5	540.0	2.2

A	B	C	D	E	F
5	9	1262.5	897.5	535.0	1.7
6	1	2407.5	1665.0	530.0	3.1
6	2	2197.5	1570.0	550.0	2.9
6	3	2080.0	1440.0	420.0	3.4
6	4	2155.0	1537.5	502.5	3.1
6	5	2042.5	1462.5	537.5	2.7
6	6	2092.5	1492.5	510.0	2.9
6	7	1842.5	1460.0	620.0	2.4
6	8	1660.0	1082.5	477.5	2.3
6	9	1720.0	1325.0	512.5	2.6
7	1	1992.5	1425.0	447.5	3.2
7	2	2207.5	1720.0	412.5	4.2
7	3	2230.0	1692.5	550.0	3.1
7	4	2175.0	1660.0	440.0	3.8
7	5	2080.0	1520.0	372.5	4.1
7	6	1972.5	1520.0	357.5	4.3
7	7	1932.5	1342.5	345.0	3.9
7	8	1845.0	1360.0	350.0	3.9
7	9	1787.5	1240.0	330.0	3.8
8	1	1505.0	1062.5	387.5	2.7
8	2	1592.5	1055.0	352.5	3.0
8	3	1665.0	1130.0	482.5	2.3
8	4	940.0	745.0	255.0	2.9
8	5	1035.0	670.0	297.5	2.3
8	6	1002.5	622.5	247.5	2.5
8	7	1005.0	680.0	250.0	2.7
8	8	1227.5	824.5	272.5	3.0
8	9	1277.5	847.5	340.0	2.5
9	1	1697.5	1235.0	325.0	3.8
9	2	1255.0	890.0	307.5	2.9
9	3	1572.5	1235.0	360.0	3.4
9	4	1167.5	855.0	267.5	3.2
9	5	1260.0	912.5	272.5	3.3
9	6	1310.0	907.5	240.0	3.8
9	7	1285.0	952.5	275.0	3.5
9	8	1410.0	1100.0	280.0	3.9
9	9	1022.5	740.0	245.0	3.0
10	1	1890.0	1370.0	450.0	3.0
10	2	1652.5	1247.5	417.5	3.0
10	3	2085.0	1505.0	440.0	3.4
10	4	2145.0	1510.0	567.5	2.7
10	5	2140.0	1585.0	535.0	3.0
10	6	2200.0	1585.0	477.5	3.3
10	7	1792.5	1192.5	455.0	2.6
10	8	1970.0	1355.0	535.0	2.5
10	9	1950.0	1360.0	475.0	2.9
11	1	1710.0	1135.0	417.5	2.7
11	2	1525.0	1100.0	417.5	2.6
11	3	1607.5	1135.0	347.5	3.3
11	4	1972.5	1382.5	470.0	2.9
11	5	1697.5	1130.0	382.5	3.0
11	6	1650.0	1192.5	402.5	3.0
11	7	1960.0	1480.0	407.5	3.6
11	8	1652.5	1192.5	402.5	3.0
11	9	1782.5	1667.5	435.0	3.8
12	1	2345.0	1710.0	430.0	4.0
12	2	2257.5	1750.0	370.0	4.7
12	3	2477.5	1770.0	402.5	4.4
12	4	2787.5	2012.5	510.0	3.9
12	5	2672.5	2070.0	505.0	3.9

A	B	C	D	E	F
12	6	2552.5	1775.0	485.0	3.7
12	7	1802.5	1325.0	315.0	4.2
12	8	2222.5	1590.0	415.0	3.8
12	9	2097.5	1462.5	382.5	3.8
13	1	1032.5	737.5	242.5	3.0
13	2	1095.0	822.5	285.0	2.9
13	3	817.5	622.0	195.0	3.2
13	4	1682.5	1295.0	502.5	2.6
13	5	1467.5	1067.5	470.0	2.3
13	6	1775.0	1310.0	552.5	2.4
13	7	1372.5	967.5	312.5	3.1
13	8	1410.0	1097.5	327.5	3.4
13	9	1332.5	882.5	332.5	2.7
14	1	1877.5	1462.5	307.5	4.8
14	2	1797.5	1372.5	337.5	4.1
14	3	1752.5	1367.5	347.5	3.9
14	4	1752.5	1215.0	332.5	3.7
14	5	1730.0	1237.5	332.5	3.7
14	6	1892.5	1402.5	352.5	4.0
14	7	2210.0	1660.0	377.5	4.4
14	8	1847.5	1465.0	460.0	3.2
14	9	2247.5	1687.5	417.5	4.0
15	1	1547.5	1102.5	325.0	3.4
15	2	1535.0	1147.5	380.0	3.0
15	3	1545.0	1192.5	422.5	2.8
15	4	1515.0	1100.0	402.5	2.7
15	5	1450.0	1147.5	372.5	3.1
15	6	1577.5	1142.5	410.0	2.8
15	7	1585.0	1115.0	330.0	3.4
15	8	1670.0	1195.0	340.0	3.5
15	9	1745.0	1172.5	327.5	3.6
16	1	2170.0	1622.5	570.0	2.8
16	2	2217.5	1615.0	472.5	3.4
16	3	2132.0	1402.0	530.0	2.6
16	4	1930.0	1377.5	517.5	2.7
16	5	1795.0	1182.5	427.5	2.8
16	6	1910.0	1395.0	520.0	2.7
16	7	2500.0	1807.5	665.0	2.7
16	8	2525.0	1840.0	587.5	3.1
16	9	2485.0	1812.5	600.0	3.0
17	1	1737.5	1210.0	402.5	3.0
17	2	2145.0	1442.5	477.5	3.0
17	3	1810.0	1180.0	400.0	3.0
17	4	2020.0	1342.5	500.0	2.7
17	5	1740.0	1195.0	545.0	2.2
17	6	1995.0	1370.0	507.5	2.7
17	7	1555.0	1052.5	327.5	3.2
17	8	1587.5	1057.5	342.5	3.1
17	9	1682.5	1280.0	395.0	3.2
18	1	2222.5	1477.5	587.5	2.5
18	2	2402.5	1740.0	577.5	3.0
18	3	2485.0	1857.5	617.5	3.0
18	4	2940.0	2075.0	645.0	3.2
18	5	2722.5	1980.0	635.0	3.1
18	6	3115.0	2192.5	802.5	2.7
18	7	2360.0	1707.5	452.5	3.8
18	8	2695.0	1877.5	432.5	4.3
18	9	2495.0	1790.0	530.0	3.4
19	1	1730.0	1187.0	655.0	1.8
19	2	2105.0	1412.5	675.0	2.1

A	B	C	D	E	F
19	3	1827.0	1150.0	512.5	2.2
19	4	1447.5	895.0	575.0	1.6
19	5	1457.5	990.0	590.0	1.7
19	6	1332.5	817.5	567.5	1.4
19	7	1752.5	1172.5	635.0	1.8
19	8	1812.5	1240.0	685.0	1.8
19	9	1715.0	1170.0	602.5	1.9
20	1	2162.5	1470.0	492.5	3.0
20	2	1987.5	1357.5	502.5	2.7
20	3	2075.0	1410.0	507.5	2.8
20	4	2072.5	1437.5	477.5	3.0
20	5	1905.0	1345.0	552.5	2.4
20	6	1955.0	1365.0	570.0	2.4
20	7	2497.5	1920.0	482.5	4.0
20	8	2652.5	1850.0	512.5	3.6
20	9	2550.0	1970.0	485.0	4.1
21	1	1362.5	1027.5	337.5	3.0
21	2	1130.0	752.5	320.0	2.4
21	3	1272.5	792.5	372.5	2.1
21	4	2402.5	1815.0	547.5	3.3
21	5	1947.5	1345.0	462.5	2.9
21	6	2372.5	1817.5	557.5	3.3
21	7	2367.5	1667.5	492.5	3.4
21	8	2417.5	1747.5	615.0	2.8
21	9	2480.0	1827.5	557.5	3.3
22	1	2525.0	2747.5	525.0	5.2
22	2	2697.5	1795.0	492.5	3.6
22	3	2645.0	1965.0	547.5	3.6
22	4	2392.5	1692.5	427.5	4.0
22	5	2490.0	1737.5	495.0	3.5
22	6	2562.5	1760.0	445.0	4.0
22	7	2972.5	2247.5	497.5	4.5
22	8	3027.5	2040.0	482.5	4.2
22	9	2752.5	1822.5	515.0	3.5
23	1	1995.0	1252.5	545.0	2.3
23	2	2075.0	1512.5	402.5	3.8
23	3	2342.5	1760.0	472.5	3.7
23	4	2110.0	1610.0	375.0	4.3
23	5	2135.0	1552.5	415.0	3.7
23	6	2060.0	1425.0	467.5	3.0
23	7	1675.0	1162.5	522.5	2.2
23	8	1647.5	1245.0	555.0	2.2
23	9	1662.5	1302.5	547.5	2.4
24	1	2240.0	1610.0	450.0	3.6
24	2	2352.0	1790.0	477.5	3.7
24	3	2222.5	1555.0	600.0	2.6
24	4	2102.5	1585.0	357.5	4.4
24	5	2082.5	1530.0	372.5	4.1
24	6	2272.5	1705.0	417.5	4.1
24	7	2707.5	1852.5	525.0	3.5
24	8	2432.5	1822.5	522.5	3.5
24	9	2300.0	1705.0	385.0	4.4
25	1	1812.5	1330.0	350.0	3.8
25	2	1810.0	1097.5	370.0	3.0
25	3	1762.5	1287.5	405.0	3.2
25	4	1932.5	1330.0	465.0	2.9
25	5	1800.0	1265.0	445.0	2.8
25	6	1617.5	1100.0	502.5	2.2
25	7	1860.0	1342.5	555.0	2.4
25	8	1840.0	1375.0	447.5	3.1

A	B	C	D	E	F
25	9	1877.5	1345.0	500.0	2.7
26	1	2517.5	1905.0	400.0	4.8
26	2	2267.5	1725.0	415.0	4.2
26	3	2492.5	1880.0	315.0	6.0
26	4	2350.0	1722.5	390.0	4.4
26	5	2442.5	1767.5	320.0	5.5
26	6	2270.0	1707.5	335.0	5.1
26	7	3072.5	2275.0	470.0	4.8
26	8	2730.0	2142.5	527.0	4.1
26	9	3055.0	2265.0	450.0	5.0
27	1	2975.0	2272.5	420.0	5.4
27	2	2792.5	2147.5	470.0	4.6
27	3	2870.0	2342.5	445.0	5.3
27	4	2440.0	1872.5	380.0	4.9
27	5	1752.5	1325.0	345.0	3.8
27	6	1702.5	1200.0	310.0	3.9
27	7	2055.0	1427.5	465.0	3.1
27	8	1740.0	1135.0	402.5	2.8
27	9	2242.5	1642.5	372.5	4.4
28	1	2112.5	1530.0	530.0	2.9
28	2	2110.0	1575.0	547.5	2.9
28	3	2062.5	1360.0	565.0	2.4
28	4	1622.5	1192.5	645.0	1.8
28	5	1667.5	1160.0	447.5	2.6
28	6	1755.0	1225.0	455.0	2.7
28	7	1752.5	1237.5	347.5	3.6
28	8	1542.5	1075.0	382.5	2.8
28	9	1372.5	1055.0	340.0	3.1
29	1	2162.5	1597.5	372.5	4.3
29	2	2470.0	1832.5	325.0	5.6
29	3	2532.5	1822.5	407.5	4.5
29	4	2527.5	1777.5	442.5	4.0
29	5	2625.0	2025.0	472.5	4.3
29	6	3180.0	2240.0	507.5	4.4
29	7	2522.5	1920.0	392.5	4.9
29	8	2465.0	1842.5	385.0	4.8
29	9	2395.0	1755.0	430.0	4.1
30	1	1432.5	1035.0	317.5	3.3
30	2	1482.5	1077.5	260.0	4.1
30	3	1320.0	970.0	297.5	3.3
30	4	1870.0	1392.5	305.0	4.6
30	5	2177.5	1585.0	550.0	2.9
30	6	2012.5	1442.5	385.0	3.7
30	7	2122.5	1495.0	500.0	3.0
30	8	2042.5	1575.0	482.5	3.3
30	9	2072.5	1525.0	440.0	3.5
31	1	2140.0	1545.0	497.5	3.1
31	2	2125.0	1397.5	482.5	2.9
31	3	2100.0	1495.0	490.0	3.1
31	4	2707.5	1780.0	522.5	3.4
31	5	2745.0	1812.5	412.5	4.4
31	6	2577.5	1895.0	447.5	4.2
31	7	1925.0	1177.5	400.0	2.9
31	8	1942.5	1337.5	407.5	3.3
31	9	1535.0	1167.5	350.0	3.3
32	1	2802.5	2070.0	535.0	3.9
32	2	2692.5	1952.5	525.0	3.7
32	3	2537.5	1832.5	545.0	3.4
32	4	3485.0	2712.5	457.5	5.9
32	5	3522.5	2730.0	565.0	4.8

A	B	C	D	E	F
32	6	3295.0	2500.0	445.0	5.6
32	7	2925.0	2180.0	440.0	5.0
32	8	2957.0	2070.0	410.0	5.0
32	9	3082.5	2175.0	432.5	5.0
33	1	1835.0	1105.0	442.5	2.5
33	2	1775.0	1170.0	452.5	2.6
33	3	1642.5	1152.5	462.5	2.5
33	4	1372.5	915.0	340.0	2.7
33	5	1422.5	1015.0	357.5	2.8
33	6	1417.5	957.5	377.5	2.5
33	7	2127.5	1490.0	590.0	2.5
33	8	2032.5	1345.0	582.5	2.3
33	9	2047.0	1510.0	627.5	2.4
34	1	2662.5	1990.0	425.0	4.7
34	2	2527.5	1902.5	515.0	3.7
34	3	2375.0	1820.0	565.0	3.2
34	4	1995.0	1480.0	322.5	4.6
34	5	1922.5	1497.5	370.0	4.0
34	6	1872.5	1460.0	415.0	3.5
34	7	2170.0	1552.5	477.5	3.3
34	8	2342.5	1840.0	535.0	3.4
34	9	2372.5	1782.5	405.0	4.4
35	1	2080.0	1412.5	437.5	3.2
35	2	2107.5	1557.5	422.5	3.7
35	3	2005.0	1415.0	455.0	3.1
35	4	1932.5	1385.0	420.0	3.3
35	5	1980.0	1430.0	450.0	3.2
35	6	2032.5	1480.0	427.5	3.5
35	7	1965.0	1410.0	502.5	2.8
35	8	2190.0	1650.0	562.5	2.9
35	9	1790.0	1362.5	435.0	3.1
36	1	2647.5	1825.0	615.0	3.0
36	2	2775.0	1860.0	502.5	3.7
36	3	2587.5	1792.5	550.0	3.3
36	4	2620.0	1875.0	602.5	3.1
36	5	2852.5	2002.5	647.5	3.1
36	6	2660.0	1850.0	682.5	2.7
36	7	2462.5	1650.0	505.0	3.3
36	8	2867.5	1977.5	602.5	3.3
36	9	2620.0	1740.0	697.5	2.5
37	1	1665.0	1112.5	490.0	2.3
37	2	1852.0	1140.0	565.0	2.0
37	3	1690.0	1257.5	412.0	3.1
37	4	1915.0	1072.5	532.5	2.0
37	5	1567.0	1042.5	425.0	2.5
37	6	1615.0	1105.0	415.0	2.7
37	7	1500.0	1035.0	522.5	2.0
37	8	1515.0	935.0	492.0	1.9
37	9	1470.0	945.0	440.0	2.1
38	1	1987.5	1460.0	430.0	3.4
38	2	1920.0	1275.0	315.0	4.0
38	3	1730.0	1320.0	392.0	3.4
38	4	1787.5	1235.0	337.5	3.7
38	5	1607.5	1172.5	310.0	3.8
38	6	1682.5	1122.5	250.0	4.5
38	7	1615.0	1182.5	292.5	4.0
38	8	1772.5	1185.0	257.5	4.6
38	9	1650.0	1195.0	350.0	3.4
39	1	2470.0	1845.0	432.5	4.3
39	2	2355.0	1665.0	470.0	3.5

A	B	C	D	E	F
39	3	2352.5	1710.0	370.0	4.6
39	4	2122.5	1452.5	302.5	4.8
39	5	2315.0	1745.0	372.5	4.7
39	6	2337.5	1717.5	477.5	3.6
39	7	1565.0	1077.5	327.5	3.3
39	8	1920.0	1337.5	312.5	4.3
39	9	1677.5	1227.5	387.5	3.2
40	1	2520.0	1872.5	400.0	4.7
40	2	2637.5	1982.5	395.0	5.0
40	3	2517.5	1702.5	380.0	4.5
40	4	2097.5	1322.5	340.0	3.9
40	5	2620.0	2000.0	487.5	4.1
40	6	2980.0	2162.5	472.5	4.6
40	7	2195.0	1627.5	365.0	4.5
40	8	2277.5	1775.0	377.0	4.7
40	9	2312.5	1660.0	307.5	5.4
41	1	1357.5	895.0	410.0	2.2
41	2	1615.0	1177.5	452.5	2.6
41	3	1392.5	932.5	447.5	2.1
41	4	1372.5	1050.0	415.0	2.5
41	5	1710.0	1182.5	462.0	2.6
41	6	1567.5	1210.0	452.5	2.7
41	7	1745.0	1190.0	552.5	2.2
41	8	1667.5	1045.0	467.5	2.2
41	9	1482.5	1052.5	510.0	2.1
42	1	2242.5	1370.0	812.5	1.7
42	2	2647.5	1807.5	727.5	2.5
42	3	2590.0	1762.5	705.0	2.5
42	4	2225.0	1652.5	535.0	3.1
42	5	2327.5	1780.0	607.5	2.9
42	6	1757.5	1265.0	592.5	2.1
42	7	2095.0	1512.5	575.0	2.6
42	8	2005.0	1377.5	467.5	2.9
42	9	1825.0	1085.0	687.5	1.6
43	1	1900.0	1447.5	500.0	2.9
43	2	2082.0	1490.0	395.0	3.8
43	3	1955.0	1452.5	450.0	3.2
43	4	1745.0	1195.0	452.5	2.6
43	5	1312.5	927.5	472.5	2.0
43	6	1752.5	1230.0	490.0	2.5
43	7	1890.0	1482.5	535.0	2.8
43	8	1837.5	1347.5	475.0	2.8
43	9	1990.0	1457.5	467.5	3.1
44	1	2205.0	1475.0	417.5	3.5
44	2	1832.5	1305.0	330.0	4.0
44	3	1877.5	1315.0	370.0	3.6
44	4	1802.5	1260.0	485.0	2.6
44	5	1310.0	877.5	282.5	3.1
44	6	1712.5	1192.5	220.0	5.4
44	7	1780.0	1242.5	387.5	3.2
44	8	1902.5	1377.5	375.0	3.7
44	9	1870.0	1322.5	387.5	3.4
45	1	1995.0	1462.5	595.0	2.5
45	2	1800.0	1077.5	607.5	1.8
45	3	1945.0	1265.0	367.5	3.4
45	4	2477.5	1790.0	635.0	2.8
45	5	1812.5	1105.0	672.5	1.6
45	6	1972.5	1267.5	662.5	1.9
45	7	1840.0	1337.5	515.0	2.6
45	8	2105.0	1607.5	465.0	3.5

A	B	C	D	E	F
45	9	1995.0	1350.0	640.0	2.1
46	1	1635.0	1132.5	402.5	2.8
46	2	3097.5	1382.5	440.0	3.1
46	3	1472.5	942.5	297.5	3.2
46	4	2107.5	1517.5	612.5	2.5
46	5	2227.5	1547.5	310.0	5.0
46	6	2105.0	1475.0	580.0	2.5
46	7	1545.0	1095.0	327.5	3.3
46	8	1525.0	1047.5	357.5	2.9
46	9	1592.5	1162.5	360.0	3.2
47	1	1750.0	1230.0	507.5	2.4
47	2	1797.5	1405.0	457.5	3.1
47	3	1722.5	1270.0	432.5	2.9
47	4	1650.0	1257.5	365.0	3.4
47	5	1692.5	1312.5	355.0	3.7
47	6	1780.0	1277.5	390.0	3.3
47	7	1720.0	1325.0	410.0	3.2
47	8	1585.0	1257.5	365.0	3.4
47	9	1615.0	1192.5	352.5	3.4
48	1	2237.5	1537.5	460.0	3.3
48	2	2272.0	1585.0	452.5	3.5
48	3	2127.5	1572.5	467.5	3.4
48	4	1852.5	1372.5	385.0	3.6
48	5	1975.0	1387.5	382.5	3.6
48	6	2070.0	1580.0	365.0	4.3
48	7	2672.5	1987.5	537.5	3.7
48	8	2542.5	1922.5	490.0	3.9
48	9	2417.5	1725.0	472.5	3.7
49	1	1600.0	1117.5	427.0	2.6
49	2	2007.5	1440.0	585.0	2.5
49	3	2030.0	1330.0	547.0	2.4
49	4	2100.0	1347.5	645.0	2.1
49	5	2087.5	1500.0	680.0	2.2
49	6	1977.5	1345.0	542.5	2.5
49	7	2142.5	1555.0	492.5	3.2
49	8	2262.5	1642.5	492.5	3.3
49	9	1987.5	1415.0	552.5	2.6
50	1	2212.5	1695.0	410.0	4.1
50	2	2185.0	1702.5	370.0	4.6
50	3	2285.0	1705.0	397.5	4.3
50	4	1800.0	1255.0	476.5	2.6
50	5	1822.5	1330.0	447.5	3.0
50	6	1960.0	1452.5	407.5	3.6
50	7	2342.5	1807.5	390.0	4.6
50	8	2285.0	1665.0	410.0	4.1
50	9	2257.5	1787.5	420.0	4.3
51	1	2217.5	1555.0	565.0	2.8
51	2	2090.0	1215.0	485.0	2.5
51	3	2035.0	1407.5	505.0	2.8
51	4	2247.5	1602.5	570.0	2.8
51	5	2155.0	1575.0	527.5	3.0
51	6	2160.0	1587.5	520.0	3.1
51	7	3047.5	1830.0	560.0	3.3
51	8	2367.5	1675.0	600.0	2.8
51	9	2452.5	1755.0	607.5	2.9
52	1	1707.5	1242.5	427.5	2.9
52	2	1605.0	1090.0	417.5	2.6
52	3	1612.5	1112.5	430.0	2.6
52	4	1435.0	1037.5	320.0	3.2
52	5	1327.5	912.5	380.0	2.4

A	B	C	D	E	F
52	6	1435.0	1022.5	317.5	3.2
52	7	1912.5	1317.5	367.5	3.6
52	8	1680.0	1177.5	412.5	2.9
52	9	1622.5	1190.0	432.5	2.8
53	1	2180.0	1587.5	452.5	3.5
53	2	2257.5	1705.0	472.5	3.6
53	3	2072.5	1637.5	407.5	4.0
53	4	2535.0	1850.0	495.0	3.7
53	5	2537.5	1900.0	415.0	4.6
53	6	2647.5	1950.0	477.5	4.1
53	7	2407.5	1780.0	507.5	3.5
53	8	2372.5	1707.5	487.5	3.5
53	9	2540.0	1845.0	472.5	3.9
54	1	2445.0	1627.5	415.0	3.9
54	2	2435.0	1820.0	242.5	7.5
54	3	2057.5	1465.0	332.5	4.4
54	4	2330.0	1630.0	480.0	3.4
54	5	2232.5	1505.0	452.5	3.3
54	6	2872.5	2117.5	335.0	6.3
54	7	2292.5	1542.5	400.0	3.9
54	8	2260.0	1417.5	345.0	4.1
54	9	1937.5	1400.0	302.5	4.6
56	1	2315.0	1560.0	497.5	3.1
56	2	2315.0	1730.0	642.5	2.7
56	3	2500.0	1747.5	577.5	3.0
56	4	1802.5	1357.5	480.0	2.8
56	5	1785.0	1262.5	490.0	2.6
56	6	1602.5	1300.0	517.5	2.5
56	7	1570.0	1085.0	452.5	2.4
56	8	1352.5	1030.0	310.0	3.3
56	9	1740.0	1257.5	370.0	3.4
57	1	2945.0	2175.0	527.5	4.1
57	2	2545.0	1875.0	555.0	3.4
57	3	2762.5	2005.0	570.0	3.5
57	4	2280.0	1570.0	367.5	4.3
57	5	2947.5	2132.5	460.0	4.6
57	6	2777.5	2090.0	450.0	4.6
57	7	2935.0	2162.5	422.5	5.1
57	8	2902.5	1445.0	530.0	2.7
57	9	2417.5	1765.0	350.0	5.0
58	1	1875.0	1357.5	490.0	2.8
58	2	1865.0	1282.5	472.5	2.7
58	3	1830.0	2177.5	415.0	5.2
58	4	1657.5	1187.5	387.5	3.1
58	5	1592.5	1192.5	392.5	3.0
58	6	1885.0	1297.5	535.0	2.4
58	7	1612.5	1070.0	367.5	2.9
58	8	1655.0	1110.0	420.0	2.6
58	9	1660.0	1097.5	385.0	2.9
59	1	1912.5	1357.5	752.5	1.8
59	2	1942.5	1287.5	727.5	1.8
59	3	1890.0	1227.5	745.0	1.6
59	4	1837.5	1242.5	495.0	2.5
59	5	1800.0	1307.5	540.0	2.4
59	6	1832.5	1275.0	427.5	3.0
59	7	1840.0	1302.5	647.5	2.0
59	8	1705.0	1205.0	620.0	1.9
59	9	1840.0	1357.5	517.5	2.6
60	1	1962.5	1415.0	515.0	2.7
60	2	1660.0	1115.0	527.5	2.1

A	B	C	D	E	F
60	3	1797.5	1397.5	532.5	2.6
60	4	1550.0	1110.0	445.0	2.5
60	5	1702.5	1252.5	370.0	3.4
60	6	1820.0	1280.0	460.0	2.8
60	7	1447.5	1062.5	465.0	2.3
60	8	1967.5	1155.0	460.0	2.5
60	9	2030.0	1415.0	447.5	3.2
61	1	1815.0	1297.5	535.0	2.4
61	2	1687.5	1260.0	470.0	2.7
61	3	1625.0	1185.0	452.5	2.6
61	4	1982.5	1332.5	590.0	2.3
61	5	1992.5	1495.0	595.0	2.5
61	6	1807.5	1280.0	587.5	2.2
61	7	2165.0	1520.0	592.5	2.6
61	8	2295.0	1542.5	710.0	2.2
61	9	2322.5	1785.0	635.0	2.8
62	1	1105.0	782.5	262.0	3.0
62	2	1072.5	922.5	302.5	3.0
62	3	1390.0	1047.5	400.0	2.6
62	4	1237.5	830.0	350.0	2.4
62	5	1712.5	1232.5	385.0	3.2
62	6	1590.0	980.0	387.5	2.5
62	7	1350.0	997.5	315.0	3.2
62	8	1210.0	935.0	305.0	3.1
62	9	1365.0	1132.5	270.0	4.2
63	1	1945.0	1470.0	580.0	2.5
63	2	1920.0	1632.5	632.5	2.6
63	3	1807.5	1345.0	570.0	2.4
63	4	1922.5	1557.5	545.0	2.9
63	5	1870.0	1372.5	577.5	2.4
63	6	1945.0	1490.0	585.0	2.5
63	7	2207.5	1612.5	632.5	2.5
63	8	2042.5	1447.5	767.5	1.9
63	9	1927.5	1322.5	675.0	2.0
64	1	2247.5	1560.0	577.5	2.7
64	2	2520.0	1775.0	602.5	2.9
64	3	2405.0	1740.0	562.5	3.1
64	4	2545.0	1765.0	550.0	3.2
64	5	2575.0	1890.0	610.0	3.1
64	6	2530.0	1725.0	642.5	2.7
64	7	1890.0	1220.0	552.5	2.2
64	8	1982.5	1425.0	575.0	2.5
64	9	2030.0	1487.5	477.5	3.1
65	1	1640.0	1082.5	337.5	3.2
65	2	1520.0	1107.5	295.0	3.8
65	3	1420.0	1042.5	285.0	3.7
65	4	2175.0	1547.5	445.0	3.5
65	5	2097.5	1590.0	482.0	3.3
65	6	2225.0	1677.5	450.0	3.7
65	7	2040.0	1515.0	435.0	3.5
65	8	1977.5	1350.0	405.0	3.3
65	9	1975.0	1435.0	390.0	3.7
66	1	2345.0	1690.0	477.5	3.5
66	2	2365.0	1740.0	512.5	3.4
66	3	2382.5	1732.5	467.5	3.7
66	4	2070.0	1467.5	500.0	2.9
66	5	2155.0	1557.5	342.5	4.5
66	6	2390.0	1685.0	427.5	3.9
66	7	1765.0	1280.0	270.0	4.7
66	8	1525.0	985.0	365.0	2.7
66	9	1520.0	992.5	367.5	2.7
67	1	2960.0	2045.0	647.5	3.2
67	2	2575.0	1727.5	730.0	2.4
67	3	2642.5	1917.5	715.0	2.7
67	4	3025.0	2060.0	685.0	3.0
67	5	2360.0	1580.0	657.5	2.4
67	6	2932.5	1980.0	590.0	3.4
67	7	1825.0	1177.5	620.0	1.9
67	8	2342.5	1540.0	690.0	2.2
67	9	2582.5	1845.0	780.0	2.4
68	1	1830.0	1325.0	470.0	2.8
68	2	1670.0	1235.0	425.0	2.9
68	3	1767.5	1322.5	410.0	3.2
68	4	1680.0	1217.5	480.0	2.5
68	5	1940.0	1467.5	442.5	3.3
68	6	1875.0	1267.5	525.0	2.4
68	7	2045.0	1452.5	505.0	2.9
68	8	1860.0	1265.0	575.0	2.2
68	9	1997.5	1455.0	460.0	3.2
69	1	1497.5	1007.5	400.0	2.5
69	2	1535.0	1002.5	430.0	2.3
69	3	1475.0	980.0	447.5	2.2
69	4	1647.5	1217.5	405.0	3.0
69	5	1645.0	1172.5	460.0	2.5
69	6	1640.0	1075.0	490.0	2.2
69	7	1555.0	1077.5	392.5	2.7
69	8	1695.0	1132.5	395.0	2.9
69	9	1800.0	1205.0	447.5	2.7
70	1	2332.5	1507.5	600.0	2.5
70	2	2420.0	1520.0	587.5	2.6
70	3	2132.5	1265.0	555.0	2.3
70	4	3145.0	1432.5	690.0	2.1
70	5	2120.0	1095.0	595.0	1.8
70	6	1732.5	1227.5	582.5	2.1
70	7	1910.0	1210.0	547.5	2.2
70	8	1652.5	1437.5	447.5	3.2
70	9	2150.0	1775.0	570.0	3.1
71	1	2630.0	1850.0	665.0	2.8
71	2	2570.0	1807.5	542.5	3.3
71	3	2507.5	1730.0	650.0	2.7
71	4	1982.5	1280.0	460.0	2.8
71	5	1947.5	1430.0	567.5	2.5
71	6	2285.0	1517.5	570.0	2.7
71	7	2567.5	1720.0	630.0	2.7
71	8	2407.5	1635.0	590.0	2.8
71	9	2132.5	1430.0	545.0	2.6
72	1	1590.0	1157.5	395.0	2.9
72	2	1877.5	1317.5	450.0	2.9
72	3	1892.5	1340.0	425.0	3.2
72	4	1472.5	1040.0	367.5	2.8
72	5	1615.0	1195.0	382.5	3.1
72	6	1640.0	1215.0	400.0	3.0
72	7	1130.0	762.5	270.0	2.8
72	8	1185.0	857.5	345.0	2.5
72	9	1032.5	755.0	150.0	5.0
73	1	2132.5	1455.0	595.0	2.4
73	2	2090.0	1505.0	552.5	2.7
73	3	1720.0	1197.5	537.5	2.2
73	4	1710.0	1150.0	540.0	2.1
73	5	1595.0	1147.5	467.5	2.5

A	B	C	D	E	F
73	6	1917.5	1450.0	562.5	2.6
73	7	1285.0	922.5	357.5	2.6
73	8	1440.0	947.5	522.5	1.8
73	9	1450.0	995.0	507.5	2.0
74	1	2247.5	1557.5	512.5	3.0
74	2	1725.0	1255.0	425.0	3.0
74	3	1435.0	1135.0	437.5	2.6
74	4	1470.0	997.5	482.5	2.1
74	5	2465.0	1667.5	662.5	2.5
74	6	1775.0	1205.0	575.0	2.1
74	7	2275.0	1545.0	620.0	2.5
74	8	1805.0	1302.5	632.5	2.1
74	9	1830.0	1385.0	682.5	2.0
75	1	2017.5	1315.0	532.5	2.5
75	2	2385.0	1782.0	522.5	3.4
75	3	2432.5	1695.0	602.5	2.8
75	4	1755.0	1220.0	537.5	2.3
75	5	1937.5	1440.0	442.5	3.3
75	6	2210.0	1552.5	520.0	3.0
75	7	2092.5	1490.0	482.5	3.1
75	8	2290.0	1592.5	582.5	2.7
75	9	2192.5	1637.5	640.0	2.6
76	1	1550.0	1050.0	412.5	2.5
76	2	1722.5	1265.0	427.5	3.0
76	3	1742.5	1170.0	427.5	2.7
76	4	1392.5	1065.0	462.5	2.3
76	5	1582.5	1135.0	525.0	2.2
76	6	2035.0	1485.0	587.5	2.5
76	7	1652.5	1210.0	535.0	2.3
76	8	1940.0	1317.5	505.0	2.6
76	9	1512.5	1055.0	487.5	2.2
77	1	1297.5	1067.5	452.5	2.4
77	2	1255.0	892.5	395.0	2.3
77	3	1335.0	905.0	425.0	2.1
77	4	1112.5	842.5	452.5	1.9
77	5	1245.0	892.5	417.5	2.1
77	6	1145.0	842.5	332.5	2.5
77	7	1100.0	807.5	410.0	2.0
77	8	1162.5	890.0	402.5	2.2
77	9	1102.5	897.5	387.5	2.3
78	1	1317.5	995.0	420.0	2.4
78	2	1472.5	1137.5	390.0	2.9
78	3	1312.5	997.5	347.5	2.9
78	4	1670.0	1252.5	515.0	2.4
78	5	1665.0	1187.5	557.5	2.1
78	6	1562.5	990.0	545.0	1.8
78	7	1522.5	1147.5	445.0	2.6
78	8	1235.0	892.5	400.0	2.2
78	9	1215.0	892.5	342.5	2.6
79	1	2290.0	1755.0	357.5	4.9
79	2	2432.5	1922.5	312.5	6.2
79	3	1845.0	1347.5	262.5	5.1
79	4	2720.0	1997.5	577.5	3.5
79	5	2475.0	1727.5	535.0	3.2
79	6	2872.5	2157.5	650.0	3.3
79	7	2727.5	2042.5	490.0	4.2
79	8	2975.0	2332.5	557.5	4.2
79	9	2625.0	2042.5	467.5	4.4
80	1	1652.5	1247.5	455.0	2.7
80	2	1340.0	1032.5	452.5	2.3
80	3	1555.0	1287.5	490.0	2.6
80	4	1265.0	920.0	337.5	2.7
80	5	1222.5	847.5	335.0	2.5
80	6	1350.0	852.5	362.5	2.4
80	7	1340.0	872.5	492.5	1.8
80	8	1340.0	915.0	397.5	2.3
80	9	1337.5	762.5	425.0	1.8
81	1	1220.0	900.0	427.5	2.1
81	2	1037.5	637.5	422.5	1.5
81	3	1375.0	867.5	467.5	1.9
81	4	1260.0	962.5	470.0	2.1
81	5	1380.0	960.0	500.0	1.9
81	6	1202.5	895.0	520.0	1.7
81	7	1410.0	1082.5	632.5	1.7
81	8	1382.5	1017.5	577.5	1.8
81	9	1432.5	962.5	502.5	1.9
82	1	1822.5	1312.5	590.0	2.2
82	2	1690.0	1232.5	577.5	2.1
82	3	1865.0	1290.0	590.0	2.2
82	4	1520.0	982.5	590.0	1.7
82	5	1190.0	747.5	515.0	1.5
82	6	1495.0	1105.0	557.5	2.0
82	7	1515.0	1030.0	555.0	1.9
82	8	1735.0	1152.5	552.5	2.1
82	9	1850.0	1290.0	640.0	2.0
83	1	2327.5	1710.0	447.5	3.8
83	2	2315.0	1647.5	660.0	2.5
83	3	1615.0	1275.0	422.5	3.0
83	4	1902.5	1305.0	537.5	2.4
83	5	2297.5	1640.0	577.5	2.8
83	6	2327.5	1615.0	640.0	2.5
83	7	2237.5	1745.0	512.5	3.4
83	8	2267.5	1652.5	480.0	3.4
83	9	2322.5	1625.0	467.0	3.5
84	1	1295.0	922.5	355.0	2.6
84	2	1502.5	1017.5	387.5	2.6
84	3	1487.5	1027.5	360.0	2.9
84	4	1825.0	1325.0	440.0	3.0
84	5	2082.5	1522.5	590.0	2.6
84	6	2110.0	1497.5	450.0	3.3
84	7	1980.0	1375.0	492.5	2.8
84	8	1592.5	1150.0	432.5	2.7
84	9	1415.0	922.5	457.5	2.0
85	1	1870.0	1262.5	595.0	2.1
85	2	1847.5	1205.0	485.0	2.5
85	3	2175.0	1612.0	502.5	3.2
85	4	1962.5	1325.0	582.5	2.3
85	5	2040.0	1440.0	495.0	2.9
85	6	1902.5	1322.5	550.0	2.4
85	7	2072.5	1467.5	392.6	3.7
85	8	2142.5	1485.0	510.0	2.9
85	9	1950.0	1272.5	540.0	2.4
86	1	2087.5	1512.5	387.5	3.9
86	2	1787.5	1197.5	477.5	2.5
86	3	2135.0	1497.5	422.5	3.5
86	4	2115.0	1560.0	347.5	4.5
86	5	1890.0	1405.0	352.5	4.0
86	6	1662.5	1052.5	350.0	3.0
86	7	2220.0	1495.0	495.0	3.0
86	8	2075.0	1395.0	527.5	2.6

A	B	C	D	E	F
86	9	2207.5	1675.0	505.0	3.3
87	1	1852.5	1205.0	622.5	1.9
87	2	2087.5	1400.0	682.5	2.1
87	3	1810.0	1227.5	630.0	1.9
87	4	1732.5	1140.0	635.0	1.8
87	5	1700.0	1070.0	560.0	1.9
87	6	1492.5	1065.0	482.5	2.2
87	7	2045.0	1492.5	762.5	2.0
87	8	1822.5	1347.5	677.5	2.0
87	9	1840.0	1367.5	720.0	1.9
88	1	1530.0	1110.0	605.0	1.8
88	2	1700.0	947.5	712.5	1.3
88	3	1442.5	992.5	707.5	1.4
88	4	1700.0	1190.0	512.5	2.3
88	5	1967.5	1362.5	487.5	2.8
88	6	1737.5	1317.5	510.0	2.6
88	7	1595.0	1147.5	475.0	2.4
88	8	1485.0	992.5	480.0	2.1
88	9	1437.5	957.5	497.5	1.9
89	1	2900.0	2130.0	595.0	3.6
89	2	2892.5	2157.5	587.5	3.7
89	3	2905.0	2072.5	532.5	3.9
89	4	2245.0	1552.5	500.0	3.1
89	5	2822.5	2072.5	720.0	2.9
89	6	2632.5	1815.0	727.5	2.5
89	7	2755.0	1920.0	685.0	2.8
89	8	2695.0	2035.0	650.0	3.1
89	9	2707.5	2087.5	625.0	3.3
90	1	977.5	735.0	212.5	3.5
90	2	1035.0	702.5	232.5	3.0
90	3	995.0	777.5	207.5	3.7
90	4	1802.5	1407.5	347.5	4.1
90	5	1970.0	1422.5	405.0	3.5
90	6	1585.0	1190.0	360.0	3.3
90	7	2122.5	1612.5	480.0	3.4
90	8	2115.0	1657.5	465.0	3.6
90	9	1925.0	1465.0	522.5	2.8
91	1	1770.0	1192.5	472.5	2.5
91	2	1337.5	972.5	457.5	2.1
91	3	1655.0	1062.5	502.5	2.1
91	4	1577.5	1080.0	535.0	2.0
91	5	1455.0	1075.0	487.5	2.2
91	6	1430.0	965.0	552.5	1.7
91	7	1947.5	1370.0	670.0	2.0
91	8	1972.5	1342.5	662.5	2.0
91	9	1847.5	1247.5	617.5	2.0
92	1	2137.5	1545.0	510.0	3.0
92	2	2487.5	1890.0	627.5	3.0
92	3	2410.0	1590.0	545.0	2.9
92	4	2287.5	1747.5	477.5	3.7
92	5	2075.0	1527.5	437.5	3.5
92	6	1790.0	1197.5	402.5	3.0
92	7	1902.5	1597.5	417.5	3.8
92	8	2485.0	1742.5	442.5	3.9
92	9	2455.0	1920.0	447.5	4.3
93	1	1907.5	1445.0	560.0	2.6
93	2	1832.5	1292.5	577.5	2.2
93	3	2032.5	1447.5	532.5	2.7
93	4	2232.5	1642.5	505.0	3.3
93	5	1832.5	1250.0	577.5	2.2

A	B	C	D	E	F
93	6	2240.0	1692.5	495.0	3.4
93	7	2135.0	1450.0	515.0	2.8
93	8	1960.0	1460.0	505.0	2.9
93	9	1832.5	1367.5	485.0	2.8
94	1	1850.0	1262.5	470.0	2.7
94	2	1742.5	1132.5	495.0	2.3
94	3	2115.0	1625.0	500.0	3.3
94	4	1925.0	1277.5	505.0	2.5
94	5	2337.5	607.5	487.0	1.2
94	6	1950.0	1410.0	490.0	2.9
94	7	2065.0	1495.0	510.0	2.9
94	8	2252.5	1590.0	427.5	3.7
94	9	1842.5	1217.5	565.0	2.2
95	1	2007.5	1427.5	687.5	2.1
95	2	2032.5	1482.5	645.0	2.3
95	3	1642.5	1010.0	595.0	1.7
95	4	1807.5	1232.5	580.0	2.1
95	5	1942.5	1437.5	592.5	2.4
95	6	1897.5	1422.5	502.5	2.8
95	7	1985.0	1387.5	632.5	2.2
95	8	1757.5	1250.0	692.5	1.8
95	9	2010.0	1477.5	637.5	2.3
96	1	1905.0	1350.0	550.0	2.5
96	2	2032.5	1580.0	532.5	3.0
96	3	2075.0	1482.5	605.0	2.5
96	4	1835.0	1090.0	612.5	1.8
96	5	1547.5	1167.5	457.5	2.6
96	6	2100.0	1337.5	662.5	2.0
96	7	2195.0	1550.0	535.0	2.9
96	8	2047.5	1297.5	530.0	2.4
96	9	2185.0	1615.0	522.5	3.1
97	1	1637.5	1145.0	525.0	2.2
97	2	1835.0	1147.5	490.0	2.3
97	3	1895.0	1350.0	525.0	2.6
97	4	2112.5	1537.5	657.5	2.3
97	5	2185.0	1537.5	587.5	2.6
97	6	2060.0	1512.5	590.0	2.6
97	7	1512.5	967.5	552.5	1.8
97	8	1527.5	1037.5	480.0	2.2
97	9	1612.5	1220.0	425.0	2.9
98	1	2437.5	1880.0	520.0	3.6
98	2	1995.0	1495.0	627.5	2.4
98	3	2202.5	1667.5	500.0	3.3
98	4	2450.0	1802.5	612.5	2.9
98	5	2070.0	1532.5	627.5	2.4
98	6	1925.0	1430.0	572.5	2.5
98	7	2145.0	1510.0	505.0	3.0
98	8	1945.0	1332.5	540.0	2.5
98	9	1977.5	1447.5	615.0	2.4
99	1	2505.0	1855.0	647.5	2.9
99	2	2622.5	1997.5	542.5	3.7
99	3	2122.5	1602.5	640.0	2.5
99	4	2260.0	1657.5	542.5	3.1
99	5	2480.0	1822.5	637.5	2.9
99	6	2245.0	1487.5	707.5	2.1
99	7	2055.0	1535.0	620.0	2.5
99	8	2377.5	1705.0	665.0	2.6
99	9	2695.0	2150.0	640.0	3.4
100	1	3047.5	2237.5	655.0	3.4
100	2	2982.5	2245.0	542.5	4.1

A	B	C	D	E	F
100	3	2975.0	2187.5	597.5	3.7
100	4	2757.5	2082.5	625.0	3.3
100	5	2962.5	2152.5	610.0	3.5
100	6	2835.0	2097.5	650.0	3.2
100	7	2807.5	1765.0	425.0	4.2
100	8	2875.0	2155.0	542.5	4.0
100	9	2857.5	2090.0	545.0	3.8
101	1	1570.0	1177.5	420.0	2.8
101	2	2042.5	1442.5	460.0	3.1
101	3	1760.0	1325.0	440.0	3.0
101	4	1707.5	1242.5	395.0	3.1
101	5	1935.0	1355.0	457.5	3.0
101	6	2302.5	1662.5	507.5	3.3
101	7	2592.5	1895.0	735.0	2.6
101	8	3085.0	2397.5	680.0	3.5
101	9	2450.0	1790.0	655.0	2.7
102	1	1717.5	1152.5	462.5	2.5
102	2	2372.5	1770.0	555.0	3.2
102	3	2197.5	1570.0	510.0	3.1
102	4	2247.5	1787.5	450.0	4.0
102	5	2065.0	1652.5	442.5	3.7
102	6	1955.0	1452.5	455.0	3.2
102	7	2462.5	1967.5	642.5	3.1
102	8	2500.0	1952.5	577.5	3.4
102	9	2275.0	1625.0	605.0	2.7
103	1	2642.5	1940.0	590.0	3.3
103	2	2240.0	1637.5	470.0	3.5
103	3	2437.5	1817.5	467.5	3.9
103	4	2905.0	2110.0	585.0	3.6
103	5	3190.0	2347.5	602.5	3.9
103	6	2425.0	1807.5	520.0	3.5
103	7	2887.5	2170.0	637.5	3.4
103	8	2765.0	2017.5	607.5	3.3
103	9	1610.0	1367.5	477.5	2.9
104	1	2882.5	1980.0	497.5	4.0
104	2	2912.5	2177.5	575.0	3.8
104	3	2955.0	2182.5	557.5	3.9
104	4	1935.0	1487.5	325.0	4.6
104	5	1820.0	1340.0	360.0	3.7
104	6	2157.5	1670.0	380.0	4.4
104	7	2357.5	1955.0	490.0	4.0
104	8	2465.0	1945.0	462.5	4.2
104	9	2437.5	1960.0	487.5	4.0
105	1	2182.5	1755.0	270.0	6.5
105	2	2082.5	1467.5	330.0	4.4
105	3	2112.5	1677.5	257.5	6.5
105	4	2115.0	1580.0	385.0	4.1
105	5	2237.0	1622.5	445.0	3.6
105	6	2347.5	1667.5	370.0	4.5
105	7	1695.0	1292.5	330.0	3.9
105	8	1352.5	895.0	257.5	3.5
105	9	1657.5	1182.5	260.0	4.5
106	1	2557.5	1800.0	565.0	3.2
106	2	2585.0	1840.0	647.5	2.8
106	3	2395.0	1767.5	725.0	2.4
106	4	2382.5	1665.0	695.0	2.4
106	5	2285.0	1607.5	617.5	2.6
106	6	2405.0	1652.5	587.5	2.8
106	7	3042.5	2060.0	647.5	3.2
106	8	2550.0	1912.5	580.0	3.3

A	B	C	D	E	F
106	9	2235.0	1645.0	587.5	2.8
107	1	1487.5	952.5	467.5	2.0
107	2	1510.0	1060.0	432.5	2.5
107	3	1572.5	1150.0	455.0	2.5
107	4	1147.5	802.5	355.0	2.3
107	5	1120.0	845.0	375.0	2.3
107	6	1282.5	877.5	410.0	2.1
107	7	1477.5	972.5	560.0	1.7
107	8	1845.0	1372.5	537.5	2.6
107	9	1555.0	947.5	625.0	1.5
108	1	2912.5	2197.5	365.0	6.0
108	2	2872.5	2315.0	387.5	6.0
108	3	2785.0	2147.5	415.0	5.2
108	4	2427.5	2050.0	375.0	5.5
108	5	2430.0	1852.5	390.0	4.8
108	6	1905.0	1425.0	317.5	4.5
108	7	2220.0	1697.5	285.0	6.0
108	8	2330.0	1807.5	315.0	5.7
108	9	2150.0	1750.0	360.0	4.9
109	1	1687.5	1280.0	402.5	3.2
109	2	1955.0	1470.0	490.0	3.0
109	3	1922.5	1462.5	495.0	3.0
109	4	2142.5	1575.0	502.5	3.1
109	5	1917.5	1220.0	475.0	2.8
109	6	2042.5	1492.5	610.0	2.4
109	7	2345.0	1647.5	625.0	2.6
109	8	2302.5	1680.0	575.0	2.9
109	9	2267.5	1760.0	610.0	2.9
110	1	1407.5	940.0	392.5	2.4
110	2	1600.0	1115.0	432.5	2.6
110	3	1285.0	862.5	415.0	2.1
110	4	1327.5	1017.5	385.0	2.6
110	5	1892.5	1297.5	465.0	2.8
110	6	2000.0	1392.5	485.0	2.9
110	7	1670.0	1075.0	407.5	2.6
110	8	1790.0	1237.5	422.5	2.9
110	9	1740.0	1197.5	435.0	2.8

Appendix 2-C

Morphological character measurements in Meesia triquetra - Cell lengths.

Where: A = site number and B = leaf number.

A	B	Cell Length (μm)				
1	1	44.2	34.8	38.7	43.7	38.5
1	2	29.6	19.2	28.3	26.3	31.1
1	3	22.9	22.5	15.4	18.5	21.0
1	4	25.4	16.3	17.1	24.0	24.2
1	5	22.9	25.6	31.1	32.3	34.8
1	6	20.8	22.1	16.0	22.5	17.1
2	1	21.0	24.4	36.7	33.8	23.8
2	2	20.4	16.9	32.1	38.5	21.5
2	3	25.8	29.6	19.8	20.2	30.4
2	4	17.7	19.6	21.7	14.0	11.9
2	5	19.0	24.0	20.6	18.5	17.9
2	6	20.8	19.0	17.1	17.9	22.7
3	1	24.8	31.5	35.6	34.8	28.1
3	2	21.3	32.3	40.6	31.0	27.9
3	3	37.1	37.5	18.7	51.5	51.9
3	4	30.2	33.5	47.9	29.2	44.0
3	5	45.2	33.7	31.0	27.5	23.8
3	6	23.7	23.1	33.7	36.3	
4	1	33.8	25.6	26.0	40.4	19.2
4	2	28.5	23.3	28.1	29.2	29.8
4	3	20.6	27.5	21.9	18.5	21.9
4	4	26.5	25.0	26.1	17.7	25.4
4	5	21.7	21.3	19.8	40.6	30.6

A	B	Cell Length (μm)				
4	6	28.7	33.1	18.7	16.9	35.6
5	1	25.6	34.8	37.9	37.7	31.7
5	2	22.5	17.7	21.9	33.3	37.9
5	3	40.8	41.1	34.2	53.5	38.8
5	4	31.3	28.5	32.7	30.2	26.9
5	5	44.8	35.4	44.6	24.2	46.9
5	6	49.2	30.6	48.7	33.8	42.1
6	1	16.0	15.8	36.3	27.9	26.5
6	2	20.4	38.1	51.3	29.4	31.0
6	3	45.8	35.6	35.0	29.8	28.7
6	4	30.6	33.1	42.7	26.5	24.8
6	5	25.6	25.8	35.0	14.8	17.9
6	6	13.7	11.3	15.4	20.6	13.7
7	1	32.7	24.0	25.4	31.9	21.5
7	2	32.5	42.9	21.0	39.0	14.8
7	3	33.3	32.1	28.7	31.5	35.2
7	4	20.0	14.4	15.2	31.1	25.0
7	5	17.5	24.2	21.0	29.8	24.6
7	6	29.8	22.1	23.3	22.3	26.1
8	1	25.4	11.5	18.8	13.3	17.5
8	2	42.5	37.7	14.4	17.1	16.0
8	3	18.5	14.2	11.0	28.3	25.4
8	4	31.5	14.4	31.3	15.6	22.5
8	5	21.0	20.2	31.7	22.5	13.8
8	6	24.0	25.2	19.4	19.0	13.1
9	1	11.3	20.6	17.5	25.2	26.9
9	2	18.3	19.2	13.5	17.1	20.0
9	3	19.6	21.5	29.2	19.2	22.3
9	4	16.9	20.4	22.7	7.3	7.3
9	5	12.5	21.1	18.8	9.8	17.7
9	6	15.6	20.2	19.8	19.4	16.9
10	1	27.1	29.0	16.7	28.1	31.3
10	2	45.4	27.1	28.1	35.0	30.2
10	3	15.4	38.1	21.0	40.0	29.6
10	4	14.0	15.4	12.9	23.8	30.0
10	5	27.9	33.3	20.2	27.5	20.4
10	6	26.9	41.1	43.7	40.4	44.8
11	1	25.6	32.3	30.8	42.7	32.7
11	2	24.8	19.8	32.7	31.3	66.0
11	3	19.2	27.5	42.9	39.4	41.9
11	4	27.1	45.8	46.3	27.5	28.5
11	5	38.1	26.9	18.7	25.2	28.7
11	6	24.2	31.0	21.3	11.0	23.3
12	1	24.6	32.5	53.3	53.7	26.7
12	2	19.0	24.2	61.9	43.1	35.4
12	3	57.3	45.2	54.6	101.0	55.4
12	4	50.4	49.4	48.1	27.1	25.4
12	5	32.5	31.3	42.5	26.5	32.3
12	6	18.8	20.6	24.0	25.8	18.5
13	1	26.3	20.2	21.9	21.5	25.8
13	2	17.9	23.1	11.5	12.5	18.7
13	3	33.8	15.2	32.3	23.3	27.5
13	4	21.5	26.0	23.7	18.3	21.5
13	5	15.0	22.9	20.2	26.1	22.5
13	6	26.7	13.5	15.0	16.0	13.7
14	1	29.0	39.2	27.9	36.0	26.7
14	2	33.8	32.1	22.3	18.5	28.3
14	3	36.3	31.0	29.6	28.7	25.8
14	4	29.2	14.8	34.6	30.4	24.8
14	5	42.5	36.5	30.4	45.6	34.8

A	B	Cell Length (μm)				
14	6	39.6	30.4	35.2	42.5	43.7
15	1	20.0	40.0	35.0	17.7	27.1
15	2	34.2	31.7	44.8	46.0	37.7
15	3	22.7	15.6	12.7	13.1	17.3
15	4	36.0	27.9	22.5	24.0	23.5
15	5	27.3	25.8	25.6	19.0	21.3
15	6	25.8	26.7	32.3	21.0	29.0
16	1	17.3	15.6	15.6	31.3	28.8
16	2	19.8	22.7	17.9	32.3	32.7
16	3	50.2	25.2	29.6	27.7	47.3
16	4	24.2	38.5	31.0	24.6	28.8
16	5	26.0	20.4	21.5	35.2	31.5
16	6	30.8	26.0	24.2	29.0	20.4
17	1	34.2	17.1	29.0	24.4	23.5
17	2	17.3	13.3	16.9	18.3	16.9
17	3	25.4	25.0	46.0	24.6	32.3
17	4	14.8	27.7	20.6	24.4	19.8
17	5	40.4	39.0	10.0	12.3	17.9
17	6	26.1	38.7	27.1	35.8	16.7
18	1	19.0	41.1	30.4	14.8	16.5
18	2	29.0	22.3	26.7	21.0	18.7
18	3	39.4	27.5	16.9	28.8	23.1
18	4	23.7	30.8	34.6	18.3	20.2
18	5	21.9	29.2	26.7	26.9	26.7
18	6	41.3	30.6	21.0	29.8	31.3
19	1	30.0	30.4	23.3	13.3	36.7
19	2	36.9	49.4	25.4	47.1	34.2
19	3	20.8	23.8	13.7	11.0	22.3
19	4	20.4	21.0	16.0	24.0	15.6
19	5	18.7	28.1	29.2	23.5	23.8
19	6	15.8	33.8	14.8	17.3	19.4
20	1	22.1	24.6	25.6	24.8	22.3
20	2	25.4	14.6	24.8	14.0	24.2
20	3	38.3	25.2	35.0	30.4	25.4
20	4	22.5	17.1	34.0	30.2	26.3
20	5	45.6	21.1	27.1	40.4	36.0
20	6	37.7	32.3	12.9	25.6	21.7
21	1	28.3	31.3	30.0	13.8	21.5
21	2	36.1	21.9	30.6	18.7	16.9
21	3	28.1	45.4	32.5	30.8	27.9
21	4	24.8	19.4	16.3	35.0	16.7
21	5	26.5	26.0	23.1	17.9	41.3
21	6	37.7	39.4	38.5	40.0	13.5
22	1	27.3	22.5	19.0	35.4	37.3
22	2	53.5	35.6	27.5	25.0	27.7
22	3	17.9	15.2	24.6	36.3	17.5
22	4	48.1	36.5	36.7	21.1	35.8
22	5	36.3	31.3	29.4	42.3	35.6
22	6	32.5	23.8	46.7	31.5	29.6
23	1	44.2	30.6	40.0	31.5	40.0
23	2	69.6	39.6	58.5	50.4	43.1
23	3	86.7	78.3	36.3	29.2	31.0
23	4	54.4	91.0	33.1	71.5	73.5
23	5	33.3	49.6	33.8	40.2	33.8
23	6	41.1	46.5	54.6	56.5	45.0
24	1	33.5	28.1	34.2	32.1	26.1
24	2	25.8	34.2	29.0	31.1	31.9
24	3	48.7	17.3	41.9	37.3	17.1
24	4	44.8	33.1	32.5	28.1	25.4
24	5	25.4	30.2	35.8	38.8	22.5

A	B	Cell Length (μm)				
24	6	22.5	28.3	25.0	24.4	24.4
25	1	30.8	26.1	23.7	35.6	31.1
25	2	26.9	26.1	24.2	25.2	33.7
25	3	36.7	24.8	14.4	28.5	18.3
25	4	27.1	35.0	42.1	22.7	29.2
25	5	20.8	22.9	31.1	33.5	31.0
25	6	35.8	44.4	37.1	28.1	24.4
26	1	17.7	16.5	39.6	36.1	24.6
26	2	34.8	27.3	53.1	37.9	37.1
26	3	34.2	28.5	14.8	28.3	24.6
26	4	38.5	32.9	29.0	28.5	26.9
26	5	33.3	24.8	19.8	36.5	35.0
26	6	31.7	36.0	34.4	36.7	33.8
27	1	35.8	49.4	20.0	33.5	34.2
27	2	47.9	53.3	29.6	48.8	34.4
27	3	41.9	37.5	47.5	70.6	41.3
27	4	45.0	51.5	50.4	35.0	33.8
27	5	36.7	22.3	20.8	29.4	29.8
27	6	72.9	73.1	69.0	37.1	22.3
28	1	22.1	45.6	17.1	26.1	28.5
28	2	23.5	21.0	26.9	24.2	14.0
28	3	25.0	22.1	33.7	20.0	18.5
28	4	40.0	19.4	36.9	25.6	22.9
28	5	58.3	28.8	41.9	76.9	48.7
28	6	26.5	34.8	21.3	22.5	35.8
29	1	36.7	47.1	37.9	41.1	27.7
29	2	48.3	37.7	36.7	45.6	42.3
29	3	30.2	44.6	44.0	32.9	60.6
29	4	47.8	34.6	33.3	47.9	52.7
29	5	42.7	55.0	38.7	44.2	27.9
29	6	37.3	52.3	46.0	29.0	29.8
30	1	31.3	38.3	26.0	24.0	24.0
30	2	22.1	18.7	29.6	26.7	41.3
30	3	29.6	36.7	27.7	28.8	26.0
30	4	10.2	42.5	26.7	32.5	19.4
30	5	21.9	23.3	25.2	16.9	21.7
30	6	17.7	10.2	15.8	13.8	26.3
31	1	17.5	22.7	40.4	31.9	31.1
31	2	20.6	29.8	16.5	11.9	21.5
31	3	30.0	22.1	21.9	19.2	19.0
31	4	33.5	49.4	21.7	19.6	24.0
31	5	29.0	29.8	13.7	11.3	19.2
31	6	23.5	28.3	19.2	13.8	16.0
32	1	75.4	24.2	28.1	46.3	39.6
32	2	58.8	38.1	32.5	62.3	54.4
32	3	27.7	31.3	57.9	43.3	38.3
32	4	53.8	34.8	46.3	41.9	24.0
32	5	50.4	36.0	48.3	43.8	40.2
32	6	51.3	47.7	50.0	36.3	16.0
33	1	16.3	18.3	38.3	37.9	41.7
33	2	33.5	22.5	21.1	21.3	17.1
33	3	21.9	21.3	15.6	44.2	28.7
33	4	35.6	42.1	32.3	15.8	16.7
33	5	24.8	30.4	29.8	43.3	32.7
33	6	31.7	19.8	25.2	18.1	24.8
34	1	37.9	26.3	22.7	33.1	27.9
34	2	25.4	26.7	27.5	26.7	26.7
34	3	41.0	30.8	34.0	23.3	19.6
34	4	36.1	49.4	35.8	24.6	43.1
34	5	28.6	58.1	36.1	36.1	30.0

A	B	Cell Length (μm)				
34	6	27.9	38.7	25.6	32.3	21.9
35	1	23.8	20.6	23.1	26.3	38.5
35	2	37.9	36.7	29.6	20.4	20.2
35	3	43.7	31.5	18.1	37.9	13.7
35	4	21.7	23.8	23.7	18.1	15.6
35	5	60.6	25.2	45.4	60.6	51.3
35	6	30.4	48.3	49.2	35.8	38.5
36	1	31.1	27.9	49.4	50.0	45.8
36	2	38.7	39.4	36.9	18.8	28.7
36	3	24.8	28.5	32.3	39.4	39.6
36	4	29.2	39.4	37.7	37.1	34.0
36	5	31.1	20.6	22.1	34.4	36.3
36	6	63.5	61.5	28.1	24.0	29.0
37	1	24.4	26.5	17.7	22.5	19.8
37	2	23.7	29.0	27.3	27.3	31.7
37	3	33.8	20.0	23.5	31.1	30.6
37	4	26.5	41.5	37.9	32.7	39.2
37	5	23.7	16.9	19.4	16.3	12.7
37	6	19.2	30.6	23.7	23.3	19.2
38	1	21.1	30.6	22.5	43.5	19.8
38	2	53.3	51.7	60.4	30.6	45.6
38	3	61.0	34.4	32.3	35.8	33.3
38	4	30.8	26.3	33.1	46.7	32.9
38	5	30.8	31.3	33.1	23.5	38.7
38	6	47.7	37.7	30.2	30.0	31.7
39	1	24.4	29.0	27.3	24.4	13.5
39	2	26.1	24.6	26.0	24.0	21.5
39	3	28.5	32.5	19.8	28.5	31.1
39	4	23.3	27.1	30.6	33.3	24.0
39	5	12.9	21.5	13.5	5.2	20.6
39	6	21.3	23.7	16.0	15.4	22.5
40	1	32.5	64.8	46.7	45.8	35.4
40	2	52.1	41.7	46.0	28.1	31.7
40	3	28.8	42.5	25.0	32.5	25.4
40	4	20.6	27.1	27.3	12.5	20.4
40	5	30.8	22.7	27.3	20.4	21.5
40	6	22.5	30.4	28.7	23.5	30.0
41	1	21.5	20.0	22.3	20.2	22.1
41	2	13.3	9.2	26.9	18.5	16.5
41	3	25.2	27.3	16.7	9.0	19.0
41	4	12.7	20.4	16.1	21.1	15.8
41	5	25.4	30.8	34.8	17.7	22.3
41	6	29.6	34.2	29.6	35.0	23.7
42	1	30.8	35.6	30.8	37.7	32.7
42	2	38.5	28.5	27.5	32.7	45.4
42	3	42.9	37.9	25.0	56.9	42.1
42	4	32.1	71.7	46.3	44.4	43.7
42	5	42.3	25.2	29.8	22.1	18.1
42	6	30.8	28.7	31.1	14.6	21.3
43	1	37.7	42.1	36.0	32.7	22.3
43	2	54.0	54.2	24.8	33.8	58.8
43	3	23.1	22.3	33.1	33.8	30.8
43	4	39.4	51.0	36.0	31.0	14.6
43	5	45.4	51.7	27.1	36.1	38.7
43	6	23.8	25.8	26.9	30.0	25.8
44	1	16.3	35.2	21.0	19.2	28.8
44	2	27.9	20.4	30.6	24.4	10.2
44	3	24.6	29.2	28.8	22.7	26.9
44	4	31.5	29.0	16.5	24.6	20.8
44	5	18.3	31.3	21.5	36.1	36.1

A	B	Cell Length (μm)				
44	6	23.3	15.6	28.8	19.8	18.3
45	1	20.0	25.0	15.8	18.1	21.0
45	2	28.1	14.4	17.3	27.5	23.3
45	3	36.7	37.9	15.0	42.3	46.3
45	4	30.4	21.3	33.5	26.0	31.5
45	5	19.2	16.0	14.4	15.4	13.8
45	6	18.5	12.1	6.5	13.7	9.6
46	1	41.0	30.0	14.2	31.9	13.8
46	2	32.7	29.0	24.2	28.5	30.4
46	3	46.1	52.5	29.2	47.7	25.6
46	4	30.2	31.1	36.3	14.4	29.8
46	5	18.5	46.0	22.1	25.6	15.4
46	6	56.1	48.5	31.7	32.1	32.1
47	1	32.5	29.4	23.3	15.6	15.8
47	2	19.6	18.7	20.0	19.4	21.1
47	3	15.2	26.0	28.8	22.9	21.1
47	4	36.1	17.7	28.6	28.3	15.2
47	5	6.9	18.1	18.7	17.7	16.7
47	6	21.9	22.3	22.7	21.1	18.3
48	1	36.7	43.7	32.1	53.5	39.8
48	2	37.5	39.8	31.3	30.2	31.5
48	3	24.4	38.1	34.8	30.6	31.5
48	4	58.3	58.5	21.7	27.1	26.7
48	5	29.2	21.1	22.1	36.0	29.2
48	6	14.4	22.9	20.6	18.5	19.2
49	1	34.0	32.1	28.5	33.3	19.4
49	2	28.3	34.6	32.7	26.9	21.1
49	3	34.8	21.3	30.6	26.1	32.9
49	4	32.3	33.3	29.4	46.7	41.9
49	5	33.7	67.7	36.1	41.0	38.7
49	6	38.5	31.9	38.1	24.6	52.7
50	1	18.7	19.0	20.6	24.8	23.1
50	2	27.3	27.3	26.1	20.6	19.2
50	3	21.7	12.5	24.6	28.7	13.7
50	4	18.5	20.8	11.0	19.6	15.6
50	5	21.0	33.3	38.7	27.9	25.4
50	6	19.2	24.6	15.8	13.8	19.4
51	1	21.5	34.4	28.1	25.8	27.9
51	2	51.3	34.0	28.3	24.8	30.6
51	3	30.2	18.8	48.8	34.8	41.3
51	4	43.5	55.4	48.4	29.6	30.2
51	5	37.3	28.8	29.0	29.8	26.5
51	6	59.4	68.8	27.9	34.8	45.0
52	1	27.7	30.6	18.5	24.8	16.7
52	2	22.5	19.4	20.8	17.7	20.8
52	3	32.5	27.7	24.8	32.9	31.3
52	4	28.5	17.9	24.8	27.5	24.2
52	5	38.8	37.5	36.5	34.0	34.6
52	6	21.5	28.1	26.7	24.4	24.2
53	1	27.1	24.4	21.3	26.3	19.6
53	2	16.1	38.3	14.4	38.3	31.7
53	3	43.5	36.3	27.1	46.3	36.0
53	4	29.6	47.3	18.8	31.0	31.5
53	5	32.9	39.8	28.5	31.5	21.5
53	6	34.8	37.7	42.7	25.2	31.9
54	1	58.5	39.8	63.8	20.2	44.2
54	2	28.3	37.1	35.4	52.1	30.2
54	3	27.3	26.9	44.0	29.2	26.5
54	4	45.4	37.5	33.8	33.3	30.0
54	5	59.0	29.2	55.8	47.9	47.7

A	B	Cell Length (μm)				
54	6	36.1	33.7	43.5	32.9	24.4
56	1	35.8	34.4	33.5	24.0	34.0
56	2	37.9	21.0	27.9	29.8	37.9
56	3	27.9	26.7	29.8	26.3	18.8
56	4	21.1	20.6	19.0	19.6	16.0
56	5	24.8	23.8	19.6	26.0	17.3
56	6	21.3	14.0	23.7	30.2	17.1
57	1	33.1	24.6	54.8	59.0	41.1
57	2	46.7	47.3	26.3	35.4	37.1
57	3	27.7	26.1	43.5	50.8	46.7
57	4	62.9	29.2	50.0	48.7	51.5
57	5	75.0	46.3	39.4	33.3	25.0
57	6	45.2	50.2	49.4	42.9	36.0
58	1	26.9	26.9	21.0	25.6	22.3
58	2	37.1	33.7	17.7	29.4	26.9
58	3	27.5	28.5	34.8	26.9	26.0
58	4	19.6	21.0	16.0	26.7	26.3
58	5	28.1	40.2	20.0	25.0	26.1
58	6	30.2	22.9	17.1	27.5	21.9
59	1	30.6	20.8	18.5	14.0	15.0
59	2	35.2	21.9	31.5	27.3	31.1
59	3	40.6	53.7	59.6	32.3	19.0
59	4	51.3	25.8	29.2	20.8	36.1
59	5	17.7	21.5	23.7	21.0	22.7
59	6	26.0	20.0	31.3	19.8	20.4
60	1	26.9	43.3	56.1	18.3	28.7
60	2	29.0	20.4	30.2	25.8	17.9
60	3	37.5	21.5	26.0	24.2	16.5
60	4	44.2	29.4	29.4	25.6	21.9
60	5	23.1	27.9	21.0	17.9	30.4
60	6	36.1	15.8	40.0	30.8	44.8
61	1	67.5	62.3	45.0	16.5	30.8
61	2	27.5	36.0	34.2	54.8	24.6
61	3	43.7	40.8	23.5	38.3	32.5
61	4	13.7	24.8	16.7	19.8	16.5
61	5	16.3	32.1	23.1	36.1	36.5
61	6	55.4	31.9	42.7	32.5	21.0
62	1	17.9	19.4	15.6	8.3	19.4
62	2	50.6	16.7	36.0	29.8	27.7
62	3	46.5	42.1	54.6	49.2	36.9
62	4	20.0	20.2	17.5	19.2	14.6
62	5	48.7	24.0	30.4	22.1	25.8
62	6	14.8	8.8	11.3	10.0	6.7
63	1	26.9	17.7	21.9	21.5	35.6
63	2	29.8	30.2	30.0	20.2	19.8
63	3	18.5	22.5	16.5	16.3	14.6
63	4	24.6	34.0	27.7	24.6	16.3
63	5	24.4	20.6	23.7	38.1	15.4
63	6	22.1	30.8	24.0	24.6	26.0
64	1	45.8	40.0	46.9	33.7	40.2
64	2	18.7	40.8	33.1	36.3	29.2
64	3	77.9	59.0	50.0	42.5	42.3
64	4	21.9	20.2	17.9	36.7	39.0
64	5	39.2	38.8	38.7	39.8	47.3
64	6	47.5	36.5	37.1	36.7	36.5
65	1	25.0	28.5	18.5	19.4	18.5
65	2	53.7	29.6	54.2	44.6	40.6
65	3	37.3	31.3	36.3	33.7	36.5
65	4	47.7	35.0	69.4	61.0	46.1
65	5	45.2	41.0	37.9	38.3	24.2

A	B	Cell Length (μm)				
65	6	20.6	34.6	16.3	20.6	28.3
66	1	41.7	34.4	28.5	32.5	67.3
66	2	36.3	42.5	47.9	36.3	33.1
66	3	27.7	34.6	37.3	22.5	27.9
66	4	25.6	29.4	52.1	48.3	24.6
66	5	16.5	38.1	20.4	40.4	42.7
66	6	46.7	30.0	33.5	41.3	43.5
67	1	21.7	27.7	27.9	20.8	33.7
67	2	20.0	16.7	17.3	31.1	14.4
67	3	22.1	37.3	41.9	31.1	44.4
67	4	31.7	28.8	37.9	36.1	33.5
67	5	33.1	24.6	36.9	24.4	35.5
67	6	52.5	49.0	24.8	22.1	31.9
68	1	24.4	16.9	20.6	16.3	24.4
68	2	26.0	15.8	16.1	17.3	19.4
68	3	14.8	24.2	21.0	10.8	19.2
68	4	29.2	24.6	25.4	28.3	14.0
68	5	14.8	18.5	22.3	13.7	13.7
68	6	24.8	12.1	18.8	22.5	12.1
69	1	10.0	14.2	16.0	17.1	15.0
69	2	16.7	18.3	21.7	23.5	21.3
69	3	32.7	19.2	18.3	15.6	16.9
69	4	23.1	20.8	31.9	36.7	17.7
69	5	19.4	22.9	31.7	23.3	18.7
69	6	35.8	33.1	31.1	31.7	19.0
70	1	12.9	21.5	19.6	9.0	12.7
70	2	20.2	22.5	23.8	18.3	16.3
70	3	24.8	19.0	14.4	14.6	17.1
70	4	21.0	17.9	28.1	20.4	21.9
70	5	21.9	25.4	24.4	24.2	10.2
70	6	29.4	31.5	30.0	38.1	31.5
71	1	21.9	29.8	41.9	41.1	37.3
71	2	35.2	32.9	45.2	38.5	31.9
71	3	20.8	21.5	46.1	26.9	30.6
71	4	36.3	33.8	26.7	20.4	25.8
71	5	46.9	37.1	36.9	38.7	46.1
71	6	53.8	40.8	41.0	36.5	29.4
72	1	39.2	37.5	17.3	24.4	25.0
72	2	36.1	18.8	32.9	28.3	27.7
72	3	16.5	19.4	31.0	32.5	34.4
72	4	16.3	19.0	29.2	25.2	28.5
72	5	39.6	37.3	22.1	28.8	28.3
72	6	36.1	17.9	35.0	22.1	34.8
73	1	23.3	18.8	16.3	16.7	19.6
73	2	31.5	46.5	23.7	23.3	15.4
73	3	26.0	27.7	24.6	30.8	25.4
73	4	21.5	28.5	23.3	22.1	21.0
73	5	23.3	26.5	8.8	13.3	16.1
73	6	16.3	17.3	15.6	14.4	13.1
74	1	81.1	84.4	36.5	50.2	53.8
74	2	34.6	24.6	21.7	21.1	18.7
74	3	30.6	25.4	18.3	20.2	17.9
74	4	70.0	60.0	41.9	38.5	39.8
74	5	64.0	32.5	58.7	29.6	31.1
74	6	18.3	24.2	25.6	27.5	26.1
75	1	33.8	70.8	23.1	36.5	30.0
75	2	57.7	38.5	45.2	28.8	26.7
75	3	29.4	28.8	28.8	25.2	32.7
75	4	28.7	35.4	24.4	29.2	24.4
75	5	32.1	28.5	45.6	25.2	34.0

A	B	Cell Length (μm)				
75	6	42.1	48.5	49.6	52.7	31.7
76	1	21.3	23.1	22.3	21.1	22.5
76	2	28.1	29.4	19.4	28.7	25.8
76	3	27.5	23.7	32.3	21.7	40.0
76	4	21.9	13.5	11.7	17.3	16.9
76	5	48.1	40.0	35.0	30.8	21.3
76	6	20.0	15.0	14.4	15.2	12.9
77	1	29.4	30.2	31.0	28.7	33.3
77	2	33.1	29.2	36.3	21.7	21.7
77	3	25.4	17.5	25.6	30.6	38.3
77	4	33.3	38.3	24.4	33.3	32.3
77	5	25.8	43.5	42.9	37.3	40.0
77	6	31.1	30.8	35.6	40.6	29.2
78	1	13.5	13.7	17.5	19.4	24.2
78	2	19.4	13.7	13.5	16.3	16.0
78	3	20.6	18.3	18.3	8.7	22.5
78	4	19.8	18.3	23.5	15.0	9.0
78	5	8.8	5.8	16.7	8.7	12.5
78	6	15.0	17.9	13.8	14.0	13.3
79	1	59.6	52.3	62.9	55.8	46.3
79	2	49.0	32.7	37.1	32.3	39.0
79	3	32.3	35.8	29.8	54.6	29.6
79	4	31.0	26.9	19.2	12.9	10.4
79	5	34.0	43.5	43.3	37.9	27.5
79	6	59.2	37.3	38.1	34.4	37.9
80	1	19.8	20.8	13.5	20.2	26.7
80	2	15.6	10.8	24.0	20.2	20.6
80	3	32.7	38.1	34.8	34.6	33.1
80	4	22.9	16.0	15.2	18.5	23.3
80	5	24.6	19.4	19.8	30.8	20.8
80	6	24.8	21.5	10.2	22.9	16.3
81	1	31.3	37.7	32.7	26.0	45.6
81	2	33.7	36.7	41.0	23.5	47.9
81	3	15.2	20.2	28.7	22.9	21.9
81	4	21.1	18.7	36.0	23.3	28.1
81	5	17.1	9.0	17.9	22.9	14.6
81	6	30.2	11.7	31.9	22.5	23.3
82	1	25.4	44.8	18.3	25.0	27.3
82	2	39.4	41.5	26.3	26.5	29.2
82	3	15.0	21.3	16.1	19.8	17.9
82	4	30.0	12.1	23.7	26.1	19.6
82	5	28.3	41.0	34.2	24.4	22.5
82	6	23.3	32.9	23.8	21.5	19.8
83	1	42.1	69.2	38.3	47.1	74.4
83	2	53.5	39.0	39.4	37.7	72.9
83	3	39.2	75.0	29.6	41.7	63.1
83	4	22.3	33.8	34.3	29.0	26.9
83	5	23.7	48.3	41.5	42.9	41.5
83	6	30.6	27.9	36.0	34.6	53.5
84	1	34.6	31.7	37.1	29.6	28.1
84	2	21.3	37.3	12.1	20.0	19.2
84	3	55.2	97.5	49.6	39.2	26.9
84	4	31.5	29.6	34.4	37.3	44.4
84	5	32.3	22.9	41.9	35.8	46.9
84	6	45.2	34.0	51.1	39.4	75.2
85	1	59.4	47.9	56.9	62.5	38.7
85	2	45.8	41.9	46.3	46.9	46.1
85	3	47.3	57.3	35.4	55.4	46.7
85	4	42.1	27.5	28.8	55.2	55.4
85	5	68.3	66.0	67.9	34.6	39.4

A	B	Cell Length (μm)				
85	6	55.2	39.2	36.1	41.0	51.3
86	1	27.5	21.9	14.6	14.2	23.1
86	2	30.0	40.6	21.1	34.4	36.1
86	3	25.0	24.8	21.7	22.9	26.3
86	4	31.5	31.7	22.9	32.9	37.5
86	5	22.7	42.3	35.8	38.1	33.1
86	6	51.3	37.9	45.0	39.2	31.9
87	1	39.2	15.6	29.8	23.3	25.8
87	2	22.7	21.7	21.3	23.5	20.4
87	3	18.7	24.6	31.0	28.3	24.0
87	4	33.7	42.5	29.6	29.6	24.4
87	5	41.9	42.5	38.3	21.1	40.6
87	6	40.6	43.1	40.8	30.0	23.8
88	1	16.5	18.5	15.8	15.4	12.7
88	2	20.0	18.1	9.2	12.5	8.3
88	3	37.3	16.5	21.9	31.3	16.3
88	4	28.7	33.3	16.7	37.3	14.8
88	5	22.9	13.3	20.6	11.9	17.1
88	6	26.5	32.9	27.3	22.1	23.3
89	1	56.7	87.7	74.0	66.3	52.5
89	2	49.6	36.0	50.0	34.6	38.3
89	3	71.3	30.6	41.5	28.3	34.0
89	4	35.8	49.2	35.2	50.4	53.3
89	5	55.8	63.7	57.9	53.3	62.5
89	6	37.5	50.8	71.9	48.5	54.8
90	1	26.5	28.7	21.5	25.8	40.2
90	2	36.9	31.3	25.0	17.9	19.0
90	3	23.3	25.4	38.8	27.5	17.3
90	4	41.1	24.0	30.8	17.9	19.4
90	5	47.9	33.1	25.4	23.5	33.3
90	6	37.7	25.4	38.8	37.9	39.0
91	1	36.1	22.7	19.6	21.1	26.5
91	2	29.4	52.7	47.5	35.6	31.3
91	3	21.7	34.8	16.3	30.0	16.1
91	4	29.8	23.3	38.1	27.5	30.4
91	5	39.6	36.7	36.7	25.5	22.5
91	6	27.7	55.2	33.1	59.6	38.7
92	1	25.4	34.0	32.1	47.7	30.4
92	2	69.4	60.0	51.1	44.2	41.5
92	3	45.8	32.7	43.5	28.7	18.5
92	4	21.5	23.5	35.8	30.6	28.5
92	5	35.6	35.4	23.1	26.7	39.8
92	6	43.3	21.7	38.7	34.2	32.1
93	1	37.9	31.1	25.8	19.0	24.0
93	2	31.9	20.4	14.6	14.2	26.5
93	3	25.0	27.5	19.2	24.6	25.0
93	4	52.9	57.5	35.6	30.0	51.3
93	5	19.4	23.3	20.2	24.2	25.0
93	6	19.0	22.3	20.2	28.7	33.8
94	1	64.2	47.5	38.7	31.0	52.5
94	2	41.3	26.0	13.3	37.3	28.1
94	3	22.9	26.7	29.6	39.2	19.4
94	4	17.5	25.8	24.4	24.0	23.8
94	5	25.2	30.8	22.7	27.3	29.8
94	6	30.8	36.7	38.7	51.5	25.2
95	1	28.5	25.2	31.3	33.8	22.7
95	2	61.5	63.5	40.6	43.5	27.7
95	3	30.0	25.4	37.3	28.1	20.4
95	4	40.6	31.0	18.5	20.4	14.8
95	5	31.3	24.8	31.5	26.0	24.2

A	B	Cell Length (μm)				
95	6	24.6	30.2	19.6	23.7	23.3
96	1	42.7	16.5	31.3	24.4	41.0
96	2	31.5	39.0	28.5	42.1	26.9
96	3	36.7	26.7	20.8	37.5	20.8
96	4	48.8	46.3	43.1	39.2	31.7
96	5	42.5	23.8	22.1	23.1	26.9
96	6	51.5	33.8	35.6	26.1	37.1
97	1	18.1	21.0	27.3	21.9	13.7
97	2	41.3	34.4	34.8	23.7	31.3
97	3	32.9	28.3	31.3	33.7	29.2
97	4	39.0	28.3	36.1	35.8	29.3
97	5	46.5	56.1	34.6	22.1	18.8
97	6	20.2	21.7	19.4	24.8	21.1
98	1	22.1	21.7	15.2	20.0	16.7
98	2	34.6	41.5	37.9	44.0	36.1
98	3	25.6	26.5	25.4	45.6	49.4
98	4	27.1	16.7	28.1	28.1	24.0
98	5	34.2	22.1	25.8	30.8	26.7
98	6	21.1	22.9	13.5	22.3	24.4
99	1	45.2	46.3	29.0	37.9	30.6
99	2	21.9	29.2	34.8	35.0	24.8
99	3	33.1	20.4	21.3	24.8	31.5
99	4	36.0	26.7	18.3	23.7	21.9
99	5	33.8	20.6	24.2	35.0	28.1
99	6	34.0	29.8	38.5	43.8	25.8
100	1	55.0	41.5	48.7	53.7	29.2
100	2	60.8	57.1	41.1	37.5	43.5
100	3	40.6	54.4	45.8	44.6	47.1
100	4	47.1	60.8	56.5	42.7	35.0
100	5	54.0	54.8	36.0	43.8	38.7
100	6	57.1	51.7	46.1	38.8	32.9
101	1	21.3	24.0	20.4	27.7	15.4
101	2	35.4	32.3	21.1	31.0	23.1
101	3	38.3	34.2	34.2	30.4	54.2
101	4	41.3	43.5	38.1	32.3	31.3
101	5	23.5	34.8	36.7	41.7	49.2
101	6	37.7	24.6	31.0	41.3	25.0
102	1	22.5	30.6	34.0	24.0	27.1
102	2	35.0	47.7	38.7	51.3	20.4
102	3	32.3	15.2	18.8	18.1	20.6
102	4	27.9	13.8	26.7	21.1	20.4
102	5	42.9	50.4	74.4	43.7	53.3
102	6	39.8	38.8	40.8	38.3	38.8
103	1	52.7	45.5	50.0	60.6	81.1
103	2	16.0	36.1	31.9	15.6	17.1
103	3	57.1	50.6	48.8	45.8	42.7
103	4	31.0	39.2	56.1	54.8	55.6
103	5	35.8	29.8	31.5	41.0	22.7
103	6	74.6	63.3	39.2	54.2	56.7
104	1	47.3	52.1	41.1	50.0	21.1
104	2	53.7	26.5	19.0	22.3	18.1
104	3	24.0	29.8	32.9	28.7	17.5
104	4	23.3	16.7	22.7	24.0	13.5
104	5	40.2	42.3	37.3	20.2	35.0
104	6	63.5	37.1	26.0	25.6	30.8
105	1	73.7	59.4	71.9	59.0	35.2
105	2	77.1	43.8	37.7	26.7	30.0
105	3	34.0	34.8	41.9	54.8	34.6
105	4	45.8	41.7	42.1	35.6	37.7
105	5	49.4	39.8	29.6	36.0	50.8

Cell Length (μm)

A	B					
105	6	54.2	57.9	52.5	52.5	58.7
106	1	26.5	22.9	21.5	24.0	21.7
106	2	25.8	35.8	32.7	28.7	27.9
106	3	26.9	26.0	25.0	19.6	24.8
106	4	23.7	37.1	41.0	30.6	24.2
106	5	18.8	25.0	23.1	17.1	23.1
106	6	29.0	31.0	22.9	17.7	17.7
107	1	31.1	10.8	13.8	27.1	28.8
107	2	8.8	26.1	12.7	7.5	16.0
107	3	17.3	18.3	25.2	17.9	19.4
107	4	13.8	12.3	11.1	12.3	10.6
107	5	26.5	25.0	21.7	22.3	25.8
107	6	20.0	23.5	20.4	24.8	14.2
108	1	35.8	47.3	45.0	41.7	40.6
108	2	36.5	36.9	38.8	41.3	39.0
108	3	34.2	64.6	59.0	54.6	35.4
108	4	59.6	54.2	30.6	35.0	24.4
108	5	45.2	27.9	34.2	34.8	23.1
108	6	55.0	49.8	51.7	45.2	42.7
109	1	32.1	29.4	18.1	14.0	27.5
109	2	29.2	26.5	24.0	20.6	19.6
109	3	13.3	25.2	10.8	11.1	28.1
109	4	16.1	28.7	25.0	18.8	24.8
109	5	40.4	39.0	33.7	28.5	27.1
109	6	30.2	24.4	30.8	25.8	24.2
110	1	15.0	9.0	14.0	13.3	13.8
110	2	20.2	30.4	27.5	17.5	14.6
110	3	17.3	8.8	16.3	19.0	16.1
110	4	27.9	16.1	23.1	33.5	20.8
110	5	29.6	20.8	27.5	18.7	37.7
110	6	42.9	32.9	23.1	20.6	32.9

Appendix 2-D

Morphological character measurements in Meesia triquetra - Cell widths.

Where A = site number and B = leaf number.

A	B	Cell width (μm)				
1	1	10.4	8.7	10.7	11.9	6.7
1	2	12.7	8.8	8.8	6.5	13.1
1	3	13.4	11.7	11.5	10.0	11.5
1	4	5.0	11.5	5.2	7.5	12.9
1	5	11.7	13.5	16.9	10.4	11.9
1	6	8.1	11.9	9.0	9.6	14.0
2	1	14.0	10.8	16.1	7.9	9.2
2	2	6.5	8.3	16.5	12.5	13.1
2	3	11.9	14.4	8.7	14.8	13.1
2	4	12.5	14.0	12.9	11.0	12.3
2	5	9.2	12.9	8.5	10.0	7.5
2	6	7.7	10.8	6.9	7.3	11.0
3	1	20.8	14.0	17.1	14.6	14.0
3	2	16.9	16.5	14.4	19.2	14.6
3	3	15.2	13.7	14.6	18.5	14.2
3	4	12.3	16.7	17.7	15.6	14.2
3	5	20.0	20.2	21.9	20.2	21.9
3	6	14.0	14.4	9.8	12.5	9.0
4	1	8.6	11.0	19.0	9.8	6.0
4	2	8.3	13.7	9.4	9.4	10.8
4	3	12.3	6.3	11.0	9.2	11.3
4	4	6.5	13.7	11.0	17.1	17.5
4	5	11.7	17.5	16.0	15.2	13.5
4	6	12.1	8.1	7.9	11.1	16.5
5	1	11.5	13.3	15.6	17.5	16.3
5	2	11.7	12.7	11.7	16.0	13.3
5	3	14.0	22.1	18.7	25.2	14.2
5	4	23.3	17.7	19.0	21.7	20.6
5	5	25.4	22.9	18.8	22.3	30.4

A	B	Cell width (μm)				
5	6	17.9	13.5	8.7	16.1	17.5
6	1	16.1	14.4	16.3	3.6	15.0
6	2	19.2	19.4	21.9	12.5	10.8
6	3	18.5	21.1	17.5	20.6	22.1
6	4	10.0	13.7	12.7	16.5	19.8
6	5	17.1	8.5	12.1	9.8	11.0
6	6	14.4	14.8	16.7	14.6	9.6
7	1	11.9	6.1	11.9	7.9	11.0
7	2	9.6	6.7	14.0	8.3	12.3
7	3	5.6	9.8	11.3	11.3	8.6
7	4	9.4	6.0	11.1	11.3	7.5
7	5	11.5	8.1	7.5	10.0	11.7
7	6	3.8	14.2	8.8	10.3	6.9
8	1	8.8	6.1	7.1	10.7	14.2
8	2	9.0	10.6	16.9	10.8	11.9
8	3	9.6	6.3	7.1	2.1	5.2
8	4	11.1	9.6	11.9	6.5	2.3
8	5	9.0	9.6	6.7	14.2	8.3
8	6	7.3	5.2	6.1	7.7	7.3
9	1	8.3	8.5	8.7	3.7	9.0
9	2	6.5	9.4	7.7	7.1	10.6
9	3	10.6	10.4	12.3	11.9	13.8
9	4	8.8	6.7	8.6	12.5	6.9
9	5	11.3	6.7	5.6	8.1	8.8
9	6	9.6	12.7	11.9	4.6	12.9
10	1	14.4	15.6	13.8	13.8	13.8
10	2	9.2	15.6	14.2	11.3	15.6
10	3	13.3	12.5	9.4	12.5	13.1
10	4	13.7	7.9	16.0	16.5	17.1
10	5	15.2	11.5	17.9	10.8	4.2
10	6	10.0	7.1	11.0	14.6	16.1
11	1	12.7	15.6	12.9	15.6	16.0
11	2	16.7	17.1	8.7	15.8	7.7
11	3	10.0	10.8	11.1	7.5	16.5
11	4	7.5	9.2	12.1	14.8	14.4
11	5	16.3	16.3	10.0	12.3	11.0
11	6	16.3	12.9	19.2	10.2	9.0
12	1	13.1	17.3	17.3	15.4	13.8
12	2	8.1	9.6	6.1	10.8	9.4
12	3	14.6	20.6	20.8	17.1	20.0
12	4	16.5	13.8	17.7	19.2	21.0
12	5	7.9	11.3	14.8	9.2	10.8
12	6	6.7	5.2	7.3	8.5	12.5
13	1	10.8	13.5	9.6	5.8	11.7
13	2	10.8	13.5	13.7	12.3	6.5
13	3	8.5	12.5	13.5	12.1	13.3
13	4	10.2	4.4	9.4	15.2	9.6
13	5	9.8	13.5	9.4	11.0	15.4
13	6	5.8	11.3	5.4	12.1	5.0
14	1	11.1	9.2	8.8	12.3	11.7
14	2	16.3	17.1	13.7	16.1	11.3
14	3	13.8	15.2	21.1	14.6	16.9
14	4	13.7	17.5	17.7	17.1	12.3
14	5	10.0	9.8	13.8	13.8	11.7
14	6	14.4	13.3	17.7	11.3	12.9
15	1	14.4	12.7	10.2	11.7	18.7
15	2	15.4	11.3	12.7	16.3	16.5
15	3	4.8	9.4	12.3	9.6	10.0
15	4	10.4	11.3	11.1	7.9	10.8
15	5	8.1	11.0	13.3	12.3	6.5

A	B	Cell Width (μm)				
15	6	11.1	8.5	11.0	10.2	10.2
16	1	11.1	9.4	17.1	18.5	17.1
16	2	15.2	13.8	11.3	13.5	11.0
16	3	14.8	15.4	11.5	8.6	10.6
16	4	10.8	7.9	13.3	8.7	7.7
16	5	14.6	11.3	9.8	7.5	7.9
16	6	13.3	16.3	14.0	12.5	15.0
17	1	6.9	13.1	8.5	13.7	6.7
17	2	8.4	7.5	7.7	7.9	9.8
17	3	9.4	10.0	8.8	11.1	12.5
17	4	11.0	6.1	8.7	11.7	14.4
17	5	3.3	3.8	11.1	12.3	12.1
17	6	12.1	9.0	11.0	7.5	10.4
18	1	18.7	9.2	16.7	11.7	18.7
18	2	13.8	17.5	18.1	11.3	12.3
18	3	13.5	13.3	14.4	11.9	16.7
18	4	16.5	8.7	10.8	21.5	16.3
18	5	16.7	11.9	12.5	13.3	8.7
18	6	21.3	11.7	19.4	14.6	16.1
19	1	13.5	11.0	16.7	11.0	8.1
19	2	12.5	10.8	18.7	13.3	13.5
19	3	15.2	11.7	15.0	14.8	6.9
19	4	12.7	12.7	12.5	11.3	14.8
19	5	8.7	11.9	13.1	8.8	10.0
19	6	13.8	15.4	10.0	13.5	13.5
20	1	13.8	15.0	12.9	12.9	11.5
20	2	15.0	10.0	13.8	11.7	7.3
20	3	12.1	12.7	11.5	11.0	14.2
20	4	10.8	12.9	13.5	10.0	14.6
20	5	6.7	13.1	15.0	9.8	14.8
20	6	6.9	7.3	12.7	8.5	6.9
21	1	8.7	7.9	11.0	14.4	10.6
21	2	6.1	6.9	6.3	8.5	9.2
21	3	12.7	11.1	10.8	7.3	11.7
21	4	8.8	9.4	11.1	8.1	12.3
21	5	6.7	7.7	9.6	7.7	9.2
21	6	11.1	10.6	11.9	12.5	9.6
22	1	15.0	11.7	12.3	10.6	9.0
22	2	7.7	10.8	19.2	14.0	13.8
22	3	12.7	14.6	10.4	11.7	12.3
22	4	11.7	14.0	13.5	15.2	12.3
22	5	8.8	13.7	13.7	7.7	5.4
22	6	3.1	5.2	9.0	5.4	9.0
23	1	17.5	24.4	22.3	21.7	25.8
23	2	15.8	14.2	18.8	14.6	10.2
23	3	15.4	19.0	15.6	13.2	12.1
23	4	11.7	18.3	15.2	16.9	17.7
23	5	14.4	18.1	18.7	15.0	16.5
23	6	12.5	14.8	16.7	13.7	11.9
24	1	13.1	13.3	13.5	9.4	13.1
24	2	7.9	17.5	9.0	9.6	10.2
24	3	6.9	8.1	11.7	8.1	6.5
24	4	13.8	14.4	11.5	4.8	8.7
24	5	15.6	12.3	9.6	11.3	14.6
24	6	10.4	8.7	8.8	8.3	13.7
25	1	14.8	11.1	10.0	11.9	10.6
25	2	8.7	9.4	15.2	16.1	17.5
25	3	15.2	12.5	13.3	13.3	7.7
25	4	13.8	12.9	10.2	11.1	10.6
25	5	11.1	11.1	14.6	11.5	17.7

A	B	Cell width (μm)				
25	6	9.0	6.0	5.0	8.8	10.8
26	1	13.3	8.7	10.6	9.8	11.1
26	2	7.5	13.1	11.5	11.7	8.3
26	3	8.7	8.1	10.4	9.0	8.3
26	4	6.0	12.5	12.1	12.9	9.6
26	5	8.7	8.3	13.1	11.3	16.7
26	6	8.5	10.8	13.7	11.7	8.8
27	1	13.1	20.2	14.8	8.7	8.7
27	2	15.6	17.5	16.0	22.3	14.4
27	3	14.0	15.0	18.8	18.1	9.0
27	4	16.0	14.6	13.3	21.0	8.8
27	5	15.2	12.5	17.9	15.2	16.7
27	6	10.0	12.7	6.3	12.9	8.1
28	1	14.2	11.1	14.6	7.9	8.6
28	2	12.9	12.1	6.5	6.5	14.8
28	3	13.3	12.3	7.5	10.6	11.9
28	4	9.0	10.0	9.4	12.1	10.6
28	5	13.8	2.3	9.4	11.5	15.6
28	6	11.7	11.3	5.8	14.2	20.6
29	1	9.2	7.9	8.3	9.2	12.1
29	2	12.3	12.9	13.8	13.1	13.3
29	3	12.1	13.3	11.3	14.4	9.6
29	4	14.4	13.5	12.9	11.1	14.0
29	5	10.2	11.9	8.8	9.6	7.7
29	6	8.3	10.6	9.0	7.3	12.1
30	1	11.0	11.7	9.0	9.4	8.8
30	2	7.7	13.7	8.5	8.1	9.6
30	3	10.8	9.8	9.2	8.1	11.5
30	4	9.8	11.7	10.4	9.0	11.9
30	5	8.1	12.3	8.7	13.5	11.1
30	6	4.4	10.8	8.7	9.2	10.2
31	1	11.3	12.7	12.9	9.6	12.3
31	2	12.3	12.9	11.0	15.8	18.3
31	3	8.8	11.5	10.6	10.2	11.0
31	4	11.3	15.6	16.3	7.1	8.8
31	5	16.0	11.3	17.1	14.2	13.8
31	6	6.1	5.4	11.5	14.6	7.7
32	1	13.1	14.4	16.3	19.4	21.5
32	2	11.5	14.8	14.2	16.7	12.7
32	3	16.5	13.6	14.0	14.4	17.7
32	4	16.9	18.7	16.7	19.4	10.6
32	5	15.4	15.8	14.2	13.1	14.2
32	6	19.2	17.1	14.4	15.6	12.3
33	1	14.2	13.7	14.4	13.8	12.7
33	2	12.7	16.1	16.1	20.4	17.9
33	3	15.4	13.3	10.2	13.8	11.5
33	4	7.7	15.8	15.8	15.0	14.4
33	5	13.5	17.1	14.2	9.4	11.0
33	6	16.7	18.1	11.5	9.0	11.0
34	1	10.4	10.0	13.3	16.0	13.1
34	2	7.7	12.9	12.1	10.4	9.8
34	3	13.3	12.9	12.9	11.7	10.8
34	4	8.7	8.5	7.3	9.4	9.8
34	5	10.8	13.3	12.7	8.7	11.3
34	6	11.7	7.9	6.0	9.6	11.1
35	1	12.1	13.3	16.7	10.8	8.7
35	2	12.3	14.0	15.2	13.1	11.9
35	3	8.8	6.1	5.8	6.3	7.7
35	4	9.2	7.9	12.9	10.0	13.1
35	5	13.8	11.9	7.5	12.1	9.2

A	B	Cell Width (μm)				
35	6	9.2	11.1	7.3	8.5	12.5
36	1	10.2	17.7	12.7	9.6	6.5
36	2	11.0	20.2	18.5	14.6	11.9
36	3	13.1	14.8	20.6	12.9	13.8
36	4	16.9	18.1	19.4	18.7	11.0
36	5	6.0	10.4	17.5	18.8	13.5
36	6	15.6	12.9	14.6	8.5	16.1
37	1	10.4	8.8	11.7	14.6	8.5
37	2	11.7	12.3	8.7	10.0	7.5
37	3	10.8	13.1	13.3	15.2	14.0
37	4	14.2	10.4	10.2	7.5	13.1
37	5	11.1	8.5	11.7	6.3	10.2
37	6	12.5	10.8	10.4	10.4	12.9
38	1	8.1	8.3	11.3	9.6	13.7
38	2	12.1	12.1	8.7	10.2	12.7
38	3	11.3	7.9	17.3	16.3	11.1
38	4	15.2	11.5	12.9	11.3	11.1
38	5	4.2	9.0	9.4	8.5	17.3
38	6	10.6	12.1	11.3	5.6	7.9
39	1	9.6	10.2	14.4	11.3	12.9
39	2	15.0	10.4	4.8	9.8	14.8
39	3	13.1	11.7	10.4	5.8	9.2
39	4	12.5	10.4	12.5	9.4	18.3
39	5	11.0	9.2	9.0	9.2	8.5
39	6	8.1	3.1	9.2	8.3	11.0
40	1	16.3	21.1	14.0	22.1	13.8
40	2	12.1	8.5	19.0	15.6	20.8
40	3	17.3	9.4	11.9	9.6	12.1
40	4	10.2	8.5	7.9	7.7	15.0
40	5	8.8	5.4	9.0	7.3	6.3
40	6	10.4	9.2	16.0	13.5	12.9
41	1	10.0	8.3	13.3	10.8	14.6
41	2	8.5	10.8	7.9	12.3	9.8
41	3	10.8	12.5	9.4	11.9	8.5
41	4	12.7	6.7	10.4	11.1	10.4
41	5	8.1	12.1	12.1	8.8	16.9
41	6	17.1	12.1	16.9	18.8	14.8
42	1	16.7	12.3	15.4	11.5	16.5
42	2	11.0	9.0	11.0	11.9	11.9
42	3	15.2	11.1	17.9	9.8	14.2
42	4	14.4	10.6	13.8	7.9	12.3
42	5	13.3	12.5	10.0	9.2	12.3
42	6	15.4	18.8	16.1	12.5	10.4
43	1	15.6	6.1	8.8	7.9	14.2
43	2	6.5	10.2	11.5	7.7	8.7
43	3	9.2	9.2	6.5	12.7	
43	4	7.7	9.8	7.7	11.5	11.9
43	5	8.3	12.1	14.4	6.0	7.9
43	6	12.7	10.4	11.5	12.5	14.4
44	1	8.7	4.4	11.0	7.3	11.9
44	2	16.7	14.0	10.2	18.7	13.3
44	3	11.9	14.4	7.9	11.0	13.8
44	4	13.8	8.8	14.0	12.5	11.7
44	5	13.3	9.4	15.6	9.6	19.0
44	6	10.2	13.5	13.1	10.6	14.2
45	1	7.9	4.8	14.2	10.4	8.5
45	2	9.0	11.5	12.5	14.4	8.1
45	3	12.9	15.6	10.0	19.0	21.1
45	4	11.7	3.1	11.0	9.8	8.5
45	5	7.7	5.8	7.7	7.5	8.5

A	B	Cell Width (μm)				
45	6	3.8	8.3	7.5	5.6	11.0
46	1	15.0	15.6	18.6	14.4	22.1
46	2	13.5	15.8	12.5	11.9	13.1
46	3	16.0	9.2	13.7	14.6	14.0
46	4	8.5	11.5	10.0	12.1	13.7
46	5	8.1	9.2	9.2	14.2	12.9
46	6	17.3	20.8	12.1	17.3	16.9
47	1	17.9	16.9	11.5	17.1	12.7
47	2	8.5	11.5	9.2	9.2	11.7
47	3	10.6	9.6	13.7	13.8	12.1
47	4	8.8	8.1	11.7	16.5	9.8
47	5	11.3	13.5	7.1	13.8	11.7
47	6	9.2	7.5	10.6	11.7	5.0
48	1	16.0	10.0	18.3	14.6	9.4
48	2	12.3	14.0	12.7	15.2	12.9
48	3	12.7	12.7	15.1	21.1	15.8
48	4	7.3	15.2	13.8	11.0	13.5
48	5	9.4	8.5	11.3	11.3	9.4
48	6	11.5	11.1	7.1	12.3	11.0
49	1	9.2	8.5	9.2	11.9	11.9
49	2	11.0	10.6	8.8	9.8	12.1
49	3	10.8	16.5	9.2	10.6	12.3
49	4	6.0	6.5	10.4	9.4	10.4
49	5	8.7	12.1	11.0	15.6	9.8
49	6	8.1	17.1	8.5	10.4	12.1
50	1	9.6	8.7	9.4	8.7	10
50	2	13.5	12.5	15.6	9	10.8
50	3	7.5	8.3	10.4	10	10.4
50	4	7.9	9.2	6.1	7.3	7.3
50	5	11.5	6.9	9.8	8.7	9.6
50	6	10.4	8.7	12.7	12.3	13.7
51	1	10.6	10.8	13.3	9.2	9.4
51	2	15.8	14.6	11.7	11.3	6.1
51	3	12.1	15.0	14.0	15.8	14.6
51	4	14.0	16.0	18.1	13.7	18.5
51	5	10.8	17.3	15.4	17.5	10.6
51	6	18.3	17.7	15.2	9.0	9.2
52	1	11.5	10.0	11.1	9.0	12.1
52	2	11.7	11.7	11.7	8.7	10.2
52	3	13.1	9.6	16.0	11.9	11.9
52	4	11.7	11.9	12.7	12.1	12.9
52	5	9.0	5.4	5.2	9.0	10.6
52	6	8.3	9.8	9.6	11.7	9.0
53	1	13.5	11.5	18.1	8.5	6.9
53	2	12.5	11.3	11.0	10.2	15.0
53	3	16.1	13.5	14.0	13.8	10.8
53	4	13.1	15.0	16.3	18.5	13.5
53	5	15.4	11.5	13.8	9.4	10.0
53	6	9.4	9.0	9.2	10.4	9.2
54	1	17.5	19.8	24.2	13.8	15.4
54	2	14.4	10.2	12.9	11.5	15.6
54	3	18.7	15.2	15.4	8.3	15.0
54	4	13.5	12.7	7.7	13.7	9.2
54	5	16.9	13.3	17.9	19.6	18.8
54	6	25.6	19.2	17.1	18.3	21.3
56	1	18.7	16.0	10.0	17.7	13.7
56	2	15.4	15.8	12.5	15.0	10.6
56	3	11.9	9.0	9.6	8.8	9.0
56	4	11.1	15.4	12.5	11.9	17.1
56	5	9.6	10.4	10.2	10.6	8.1

A	B	Cell Width (μm)				
56	6	11.1	8.8	13.5	10.2	13.8
57	1	15.2	16.9	16.0	16.0	16.3
57	2	16.1	14.2	24.2	14.8	18.8
57	3	14.8	16.3	11.5	16.3	12.7
57	4	19.4	13.3	12.1	9.8	10.0
57	5	16.5	15.2	11.7	15.4	13.1
57	6	14.0	15.8	15.4	18.3	9.6
58	1	12.3	17.1	15.6	8.8	11.1
58	2	19.0	14.4	16.9	12.1	9.4
58	3	14.4	12.5	10.6	10.4	10.6
58	4	5.6	7.7	12.3	7.9	7.3
58	5	8.3	8.1	13.1	9.4	9.4
58	6	11.3	10.2	10.0	9.4	10.4
59	1	15.4	19.2	17.3	14.8	16.1
59	2	16.0	20.6	11.5	19.8	14.0
59	3	8.8	12.3	8.1	6.9	10.0
59	4	21.1	15.0	16.1	18.7	10.4
59	5	8.1	10.6	11.7	11.0	10.0
59	6	14.8	15.4	11.9	11.5	9.2
60	1	16.1	12.9	13.3	18.5	19.2
60	2	12.9	5.0	8.3	16.0	15.0
60	3	11.3	7.3	7.7	11.9	7.7
60	4	13.3	15.8	13.7	12.7	13.1
60	5	19.4	16.9	20.0	19.0	13.8
60	6	10.8	16.7	11.3	13.8	14.8
61	1	17.5	18.8	22.3	8.3	13.3
61	2	15.4	10.2	16.5	12.7	15.8
61	3	21.3	11.7	13.8	10.8	17.1
61	4	13.8	12.9	16.5	17.5	11.7
61	5	16.1	15.8	10.4	15.0	19.8
61	6	17.3	11.5	10.0	9.6	16.5
62	1	10.8	10.0	13.5	7.9	11.5
62	2	8.8	6.7	8.5	13.1	7.3
62	3	15.8	9.0	13.3	12.3	9.4
62	4	9.0	4.2	7.7	3.8	5.8
62	5	17.3	13.8	11.0	15.8	10.6
62	6	3.7	7.3	9.0	3.7	6.0
63	1	11.7	7.1	7.7	10.8	14.0
63	2	11.0	10.8	8.3	17.3	13.5
63	3	10.4	13.7	11.0	13.1	6.3
63	4	17.3	11.3	17.3	20.6	13.5
63	5	18.5	14.0	15.4	14.6	9.8
63	6	13.3	14.8	12.7	21.1	15.4
64	1	16.1	17.7	12.5	10.2	11.9
64	2	8.3	8.8	11.9	9.6	13.3
64	3	12.1	12.5	12.7	13.1	9.6
64	4	15.6	19.6	17.9	14.2	22.1
64	5	17.5	20.0	13.5	13.7	17.9
64	6	13.8	13.5	13.5	10.6	9.0
65	1	8.1	9.0	11.3	8.5	6.7
65	2	10.8	8.5	9.4	9.0	10.0
65	3	9.6	6.7	10.2	14.8	16.0
65	4	11.9	15.4	6.3	11.7	13.1
65	5	13.7	11.1	11.9	13.8	14.0
65	6	6.0	10.0	11.1	6.9	12.3
66	1	14.0	12.9	9.0	13.3	15.8
66	2	11.3	13.3	17.3	8.1	18.8
66	3	14.6	11.0	7.9	18.1	14.0
66	4	14.0	13.7	10.8	13.3	13.5
66	5	8.3	6.9	16.0	13.5	20.8

A	B	Cell Width (μm)				
66	6	11.1	7.5	11.5	16.5	11.1
67	1	15.8	14.0	11.0	17.5	10.8
67	2	12.7	7.5	12.3	14.0	10.4
67	3	14.8	11.9	19.0	14.8	14.2
67	4	11.5	14.8	9.2	11.9	18.1
67	5	12.3	14.4	6.9	5.4	15.4
67	6	10.8	16.5	16.3	8.1	9.0
68	1	11.9	3.5	11.1	3.5	5.8
68	2	10.6	12.3	10.4	13.5	9.8
68	3	6.0	8.5	4.8	13.3	9.0
68	4	13.5	5.2	9.8	4.8	10.4
68	5	9.8	11.1	10.2	13.3	12.1
68	6	13.7	9.2	8.8	14.2	10.0
69	1	9.8	18.5	19.6	15.2	11.3
69	2	8.8	16.3	17.5	11.5	12.3
69	3	15.0	9.8	9.8	14.6	10.2
69	4	19.4	6.0	7.9	13.3	12.7
69	5	16.3	11.5	14.2	10.8	15.0
69	6	12.1	20.4	17.9	10.4	14.4
70	1	10.6	13.8	7.7	7.7	9.0
70	2	13.1	11.9	14.6	10.0	13.3
70	3	16.0	13.3	7.1	10.8	10.2
70	4	16.3	16.0	17.3	16.5	14.2
70	5	11.5	12.9	8.7	9.8	7.9
70	6	13.8	12.7	14.8	12.3	10.0
71	1	13.7	12.9	15.4	11.9	14.0
71	2	14.4	18.3	13.8	10.0	16.3
71	3	13.8	15.2	16.9	13.7	14.0
71	4	11.9	15.4	17.1	13.1	15.0
71	5	12.9	12.1	16.9	21.7	13.1
71	6	13.1	11.3	18.8	17.3	11.3
72	1	8.5	7.7	8.7	15.4	8.7
72	2	6.3	8.3	12.1	7.5	10.8
72	3	5.4	10.6	8.3	9.2	11.3
72	4	8.7	12.5	8.3	10.4	10.6
72	5	13.1	12.9	15.6	10.0	8.3
72	6	7.5	14.8	12.9	11.9	10.0
73	1	10.2	12.1	13.3	5.8	12.3
73	2	13.3	10.4	11.7	9.8	11.1
73	3	15.2	11.3	14.8	13.5	15.8
73	4	16.3	18.8	21.1	21.7	17.7
73	5	14.8	12.9	14.6	10.8	11.5
73	6	7.9	9.6	9.2	9.0	10.0
74	1	21.3	18.8	23.1	13.1	13.5
74	2	10.0	10.6	13.5	12.5	14.4
74	3	10.2	11.9	8.3	8.1	7.3
74	4	16.3	16.0	16.0	11.7	18.8
74	5	16.7	14.0	21.1	19.2	13.7
74	6	8.8	11.7	9.8	9.2	9.2
75	1	15.8	16.0	9.8	12.9	17.3
75	2	15.6	10.4	12.9	14.6	11.0
75	3	16.1	7.5	14.0	12.9	14.4
75	4	15.6	11.5	13.7	7.9	14.8
75	5	11.5	11.0	9.8	12.7	16.7
75	6	18.5	13.1	14.6	9.4	13.8
76	1	7.3	7.5	12.9	11.0	13.1
76	2	10.8	11.0	11.5	21.0	13.3
76	3	16.1	14.2	12.1	16.7	11.3
76	4	11.3	17.5	10.2	14.4	16.9
76	5	17.1	17.9	12.1	14.2	11.0

A	B	Cell Width (μm)				
76	6	11.9	11.0	9.0	5.6	8.1
77	1	7.1	13.1	16.0	17.7	10.6
77	2	13.1	22.9	12.5	14.2	17.3
77	3	10.0	11.9	14.6	8.7	13.7
77	4	16.7	16.5	12.1	15.6	17.7
77	5	10.4	9.6	18.3	8.5	16.0
77	6	15.0	19.4	9.6	11.3	17.9
78	1	10.2	6.1	8.7	8.1	11.0
78	2	14.0	16.9	7.7	6.9	15.8
78	3	12.5	11.1	9.0	8.3	13.3
78	4	14.6	9.2	8.1	16.0	6.0
78	5	14.0	11.5	9.8	12.7	14.8
78	6	7.1	7.3	7.5	11.0	12.3
79	1	21.5	16.5	20.6	18.1	15.0
79	2	11.5	17.3	16.1	16.1	13.1
79	3	11.5	8.3	13.3	10.4	7.7
79	4	8.5	8.7	10.2	10.4	7.7
79	5	11.0	8.8	13.3	10.4	14.8
79	6	11.7	15.4	13.5	14.0	17.1
80	1	9.6	7.3	6.7	7.5	8.1
80	2	11.0	14.4	13.8	9.6	11.9
80	3	9.0	10.2	9.4	13.3	10.4
80	4	12.1	13.3	13.1	14.0	12.1
80	5	14.0	10.8	12.9	13.1	12.5
80	6	10.6	11.7	11.7	5.6	9.2
81	1	16.1	15.2	17.7	18.7	16.3
81	2	18.5	11.3	14.4	13.5	16.3
81	3	11.0	15.0	14.8	13.7	14.8
81	4	16.0	11.3	20.6	12.1	12.9
81	5	21.1	11.1	10.2	4.8	11.7
81	6	9.2	14.0	17.5	17.3	12.3
82	1	13.1	5.8	10.2	20.0	11.1
82	2	14.4	8.7	13.7	13.5	11.0
82	3	11.1	11.7	11.1	14.4	13.5
82	4	11.5	16.0	12.9	11.0	8.5
82	5	16.1	9.8	12.3	15.2	11.0
82	6	5.2	10.0	7.3	11.3	8.1
83	1	12.5	23.7	16.9	16.3	21.5
83	2	16.7	23.5	16.0	27.3	19.0
83	3	15.2	19.2	24.0	11.1	19.4
83	4	20.2	22.3	16.7	11.1	11.1
83	5	20.0	19.4	21.1	12.1	20.2
83	6	15.6	23.1	20.4	18.1	18.8
84	1	13.7	11.0	15.2	17.3	18.3
84	2	15.4	14.8	17.7	12.9	13.7
84	3	26.9	22.3	27.1	14.6	17.1
84	4	18.7	11.3	22.3	9.0	24.8
84	5	18.5	19.2	14.0	20.6	14.2
84	6	7.9	10.8	23.1	11.7	17.3
85	1	21.5	16.7	14.6	13.7	12.7
85	2	14.0	17.1	16.9	18.5	29.2
85	3	22.3	21.7	21.9	14.6	18.8
85	4	16.5	14.0	21.0	20.2	14.2
85	5	12.7	15.6	16.9	16.1	12.9
85	6	18.3	23.7	21.0	17.1	17.1
86	1	11.9	8.3	9.2	6.1	7.5
86	2	42.7	14.4	16.9	13.1	15.0
86	3	9.4	11.3	9.8	11.3	12.1
86	4	23.3	14.2	16.1	14.4	14.6
86	5	7.3	16.3	12.7	10.0	16.1

A	B	Cell width (μm)				
86	6	12.7	9.4	8.5	11.7	10.0
87	1	10.6	13.7	12.5	16.7	10.8
87	2	12.3	19.6	14.4	11.3	13.5
87	3	10.6	12.7	13.5	15.4	10.8
87	4	11.0	14.6	10.8	11.7	9.4
87	5	14.4	14.2	13.5	12.3	11.3
87	6	11.1	15.0	8.5	14.8	10.4
88	1	9.0	12.5	10.4	12.1	8.5
88	2	4.0	5.8	8.5	8.8	10.2
88	3	17.3	8.3	8.5	16.0	14.4
88	4	12.3	9.8	13.1	14.8	14.2
88	5	11.0	14.8	9.6	13.7	13.7
88	6	10.8	10.4	7.7	10.2	11.5
89	1	18.5	18.5	17.5	19.6	20.6
89	2	18.1	9.0	9.4	21.0	12.5
89	3	13.8	11.9	18.3	18.1	13.8
89	4	10.0	20.4	19.4	20.0	16.0
89	5	12.3	19.4	12.5	22.5	27.1
89	6	20.0	19.2	16.3	19.6	22.5
90	1	6.5	10.2	8.8	13.1	7.1
90	2	10.0	9.2	9.0	7.1	10.2
90	3	9.0	11.1	11.3	9.6	8.7
90	4	8.1	16.0	7.5	6.7	7.3
90	5	11.5	16.5	9.4	8.3	10.0
90	6	10.4	6.1	10.0	12.3	10.2
91	1	13.3	8.7	11.9	18.5	15.6
91	2	11.0	11.9	9.0	6.1	12.1
91	3	11.7	9.6	8.3	9.0	10.2
91	4	10.0	14.6	17.3	14.6	14.4
91	5	16.7	19.8	22.5	16.5	11.7
91	6	19.8	17.1	9.8	13.3	17.7
92	1	12.7	11.7	10.6	13.5	19.0
92	2	15.0	17.1	10.0	7.5	10.6
92	3	12.3	10.4	6.7	11.9	10.2
92	4	14.4	9.0	11.9	8.1	11.0
92	5	8.5	12.3	13.3	14.8	8.8
92	6	7.9	12.5	20.0	16.3	9.4
93	1	8.7	10.6	11.5	9.8	8.5
93	2	5.4	7.7	7.3	8.3	7.5
93	3	11.4	12.1	7.1	9.0	9.0
93	4	10.6	12.3	12.5	6.7	7.3
93	5	6.9	11.0	10.0	11.3	10.8
93	6	5.8	5.8	13.5	10.0	13.8
94	1	16.0	8.1	9.2	10.8	9.6
94	2	14.4	9.8	17.7	11.3	11.7
94	3	14.0	20.8	15.4	12.3	16.0
94	4	14.4	10.8	11.3	13.7	9.6
94	5	9.6	8.8	5.6	8.5	7.5
94	6	14.6	16.7	16.9	12.7	12.1
95	1	14.6	8.8	11.7	10.6	15.2
95	2	14.4	12.7	16.9	7.3	5.4
95	3	12.5	15.8	17.3	12.9	14.6
95	4	12.1	11.1	11.5	11.0	7.5
95	5	14.2	13.5	14.2	12.3	13.1
95	6	13.7	15.2	14.8	13.3	9.4
96	1	19.6	21.3	17.9	17.3	20.0
96	2	11.3	8.1	11.5	11.0	10.0
96	3	17.5	10.6	14.2	16.7	13.7
96	4	14.0	14.6	9.4	11.5	10.6
96	5	14.8	17.9	12.1	10.6	16.5

A	B	Cell width (μm)				
96	6	17.9	11.9	18.3	13.7	13.1
97	1	13.3	11.9	8.7	13.1	12.9
97	2	12.7	15.6	8.8	9.6	7.5
97	3	7.1	7.3	8.8	11.3	9.8
97	4	15.0	14.0	19.8	14.6	13.5
97	5	16.9	15.0	12.7	11.9	9.0
97	6	14.0	12.5	12.9	13.8	16.3
98	1	9.8	9.4	13.1	17.1	14.2
98	2	16.7	16.3	13.5	13.7	11.9
98	3	17.7	16.5	13.3	17.3	18.3
98	4	13.0	11.0	13.8	12.9	13.7
98	5	10.0	12.9	14.0	16.1	13.3
98	6	11.0	12.5	10.0	9.6	8.1
99	1	15.2	22.9	10.0	13.7	13.1
99	2	14.2	11.5	15.2	12.3	7.9
99	3	13.1	18.8	21.0	19.6	17.9
99	4	18.5	12.3	11.3	13.5	11.9
99	5	17.5	13.7	16.0	11.3	13.7
99	6	21.5	14.0	17.1	23.7	16.5
100	1	18.1	19.0	20.2	21.9	17.9
100	2	20.6	21.7	23.3	23.8	26.3
100	3	23.1	18.8	16.3	23.1	17.3
100	4	20.0	17.9	13.8	16.1	17.1
100	5	17.7	22.5	20.8	12.5	22.3
100	6	23.7	17.1	22.5	16.9	19.2
101	1	14.6	14.6	15.0	11.5	11.0
101	2	13.3	14.0	14.4	13.7	11.5
101	3	11.9	11.7	14.0	16.0	13.3
101	4	14.2	12.9	14.4	14.2	13.3
101	5	11.9	9.8	13.7	10.6	13.7
101	6	11.1	11.0	14.6	15.2	12.3
102	1	20.8	16.9	20.4	14.8	17.7
102	2	13.3	11.5	14.6	14.4	7.3
102	3	8.5	6.7	11.9	7.5	8.3
102	4	8.5	3.8	7.9	7.5	13.3
102	5	16.0	19.8	23.7	20.4	14.6
102	6	18.3	18.1	22.7	18.1	12.5
103	1	11.1	15.0	14.2	13.8	15.8
103	2	13.8	9.0	5.4	4.0	12.5
103	3	17.3	14.2	8.7	6.5	14.0
103	4	11.5	10.0	13.8	12.1	9.6
103	5	12.5	7.3	7.1	8.3	8.1
103	6	15.2	16.7	16.0	12.5	12.3
104	1	11.3	10.6	9.6	6.9	8.3
104	2	14.2	13.5	11.0	10.8	9.2
104	3	11.5	6.9	11.0	4.8	5.2
104	4	7.3	6.0	6.9	9.8	8.7
104	5	9.0	9.6	10.4	5.4	7.1
104	6	5.6	15.0	10.6	8.8	13.3
105	1	13.5	11.7	9.0	11.5	8.8
105	2	12.7	14.8	15.2	12.3	7.3
105	3	13.7	11.9	16.5	12.5	10.0
105	4	10.2	9.8	12.7	7.1	8.1
105	5	11.7	10.8	15.6	13.5	7.5
105	6	15.4	16.3	15.8	21.0	16.0
106	1	14.6	17.1	11.1	11.7	12.7
106	2	12.9	13.8	18.8	14.6	14.4
106	3	12.3	13.5	13.7	15.0	14.4
106	4	12.3	17.9	6.5	4.6	13.3
106	5	10.2	11.1	9.0	7.9	12.3

A	B	Cell width (μm)				
106	6	11.3	15.8	14.8	8.3	10.6
107	1	7.3	11.0	12.5	14.2	9.8
107	2	8.3	4.0	6.5	11.1	8.5
107	3	9.0	7.1	11.5	10.4	6.1
107	4	5.4	4.4	5.6	5.4	8.3
107	5	9.6	12.7	11.5	9.8	14.0
107	6	9.6	12.5	6.9	8.5	10.4
108	1	4.8	6.7	10.0	19.8	14.2
108	2	13.5	12.1	16.9	6.1	17.5
108	3	18.1	10.6	12.9	17.9	17.7
108	4	13.1	10.0	13.3	6.5	7.3
108	5	10.4	8.1	6.7	7.5	14.8
108	6	12.9	17.3	17.5	11.1	15.6
109	1	13.3	15.2	7.5	10.8	6.5
109	2	10.2	7.3	12.3	9.0	8.5
109	3	13.5	14.4	11.5	11.0	6.7
109	4	10.8	11.3	8.1	11.0	8.7
109	5	12.1	14.2	8.3	4.8	10.8
109	6	15.4	15.8	15.8	9.8	14.8
110	1	6.5	6.0	5.4	8.5	7.3
110	2	18.1	9.6	11.7	13.1	11.9
110	3	4.4	10.4	7.7	7.1	8.8
110	4	7.3	6.1	5.8	6.9	10.6
110	5	9.8	6.3	10.2	8.5	6.9
110	6	10.2	11.5	10.6	11.7	13.7

Appendix 3-A

Growth in Meesia triquetra in a controlled environment - Primary stem elongation.

Where A = treatment (1 = arctic plants, arctic water, low nitrogen; 2 = arctic plants, arctic water, high nitrogen; 3 = arctic plants, boreal water, low nitrogen, 4 = arctic plants, boreal water, high nitrogen; 5 = boreal plants, arctic water, low nitrogen; 6 = boreal plants, arctic water, high nitrogen; 7 = boreal plants, boreal water, low nitrogen, 8 = boreal plants, boreal water, high nitrogen) and B = replicate.

A	B	Growth (mm)									
1	1	1	3	3	0	0	1	0	0	2	1
1	2	3	0	0	0	1	0	2	0	2	0
1	3	1	2	3	0	1	0	1	0	0	4
1	4	0	2	2	1	0	0	0	1	0	0
1	5	0	2	0	2	3	0	2	1	0	0
1	6	1	0	0	0	0	0	0	1	3	1
1	7	1	2	2	2	4	0	5	2	3	2
1	8	1	1	2	0	2	3	3	1	5	0
2	1	0	3	0	0	0	0	0	1	0	3
2	2	2	0	0	0	0	0	0	2	1	0
2	3	0	5	3	0	2	3	2	3	0	1
2	4	0	0	0	0	3	0	3	4	0	1
2	5	0	0	1	2	1	1	2	0	2	2
2	6	1	0	2	1	2	5	0	0	4	0
2	7	0	1	0	5	0	4	3	4	2	3
2	8	0	0	2	3	5	0	0	0	3	1
3	1	2	0	1	1	2	3	0	2	1	4
3	2	2	0	0	1	0	3	2	2	0	2
3	3	0	4	0	0	0	2	1	0	4	0
3	4	1	3	2	1	1	1	2	1	1	0
3	5	2	3	3	1	2	3	4	3	2	0
3	6	0	0	0	3	0	4	0	0	3	2
3	7	0	2	0	0	0	2	0	0	2	0
3	8	0	1	0	3	4	3	2	4	4	0
4	1	0	0	0	0	0	3	2	2	2	1
4	2	2	0	0	3	1	2	3	0	0	0
4	3	0	1	0	0	3	3	3	0	3	1
4	4	0	1	4	1	3	3	3	0	0	3
4	5	2	1	1	3	2	3	2	1	0	0
4	6	0	1	2	2	0	2	2	0	0	0
4	7	0	0	1	0	1	1	2	0	2	0
4	8	1	0	2	3	1	2	2	0	3	0

A	B	Growth (mm)									
5	1	7	5	8	11	10	8	11	11	8	13
5	2	1	12	9	9	11	6	3	0	14	6
5	3	0	7	1	5	7	8	8	8	13	0
5	4	9	5	3	5	0	8	10	12	4	9
5	5	5	6	6	0	5	6	7	0	7	2
5	6	11	2	9	2	8	7	9	8	4	5
5	7	2	11	12	0	12	7	0	13	14	11
5	8	10	4	5	0	0	11	0	3	2	0
6	1	6	7	11	6	8	8	8	9	2	8
6	2	5	10	9	9	10	0	10	4	0	6
6	3	2	1	9	3	0	0	2	1	1	1
6	4	7	4	2	8	6	4	2	10	0	7
6	5	6	0	0	1	0	6	9	7	3	0
6	6	11	11	10	4	8	9	2	10	7	0
6	7	0	12	11	1	0	6	2	0	10	0
6	8	0	0	0	4	0	6	1	9	0	5
7	1	7	6	6	5	9	3	7	7	9	9
7	2	9	8	4	12	10	7	0	0	13	5
7	3	4	0	0	10	11	11	9	11	11	9
7	4	12	12	13	13	11	0	6	0	11	6
7	5	0	7	7	2	4	3	4	0	0	6
7	6	9	9	1	7	14	7	9	3	0	7
7	7	12	4	0	0	0	10	10	11	8	9
7	8	7	9	8	6	10	0	0	8	9	1
8	1	0	8	4	7	6	9	8	5	7	8
8	2	9	13	12	7	0	9	4	6	8	0
8	3	4	9	3	0	5	10	5	6	10	1
8	4	7	7	8	7	0	0	4	4	9	11
8	5	0	0	3	3	4	6	9	4	7	4
8	6	2	2	6	0	1	9	9	7	0	1
8	7	1	12	9	9	11	11	10	12	9	5
8	8	12	7	1	0	10	7	12	11	0	

Appendix 3-B

Growth in Meesia triquetra in a controlled environment - Secondary stem elongation.

Where A = plant (1 = arctic and 2 = boreal), B = water (1 = arctic and 2 = boreal), C = nitrogen treatment (1 = low and 2 = high).

A	B	C	D	Growth (mm)									
1	1	1	1	1	3	3	0	0	1	0	0	2	1
1	1	1	2	3	0	0	0	1	0	2	0	2	0
1	1	1	3	1	2	3	0	1	0	1	0	0	4
1	1	1	4	0	2	2	1	0	0	0	1	0	0
1	1	1	5	0	2	0	2	3	0	2	1	0	0
1	1	1	6	1	0	0	0	0	0	0	1	3	1
1	1	1	7	1	2	2	2	4	0	7	2	3	2
1	1	1	8	1	1	2	0	2	3	3	1	9	0
1	1	2	1	0	3	0	0	0	3	0	1	0	3
1	1	2	2	2	0	0	0	0	0	0	2	1	0
1	1	2	3	0	5	3	6	2	3	2	3	13	1
1	1	2	4	5	0	0	0	3	0	3	4	0	1
1	1	2	5	0	0	1	2	1	1	2	0	2	2
1	1	2	6	1	0	2	1	2	5	0	0	4	0
1	1	2	7	0	1	0	5	0	4	3	4	2	3
1	1	2	8	0	0	2	3	5	0	0	0	3	1
1	2	1	1	2	0	1	1	2	3	0	2	1	4
1	2	1	2	2	0	0	1	0	3	2	2	0	2
1	2	1	3	0	4	0	5	0	2	1	0	4	0
1	2	1	4	1	3	2	1	4	1	2	1	1	0
1	2	1	5	2	3	3	1	2	3	8	3	2	0
1	2	1	6	0	0	0	7	0	12	0	0	3	2
1	2	1	7	0	2	0	0	0	2	0	0	2	0
1	2	1	8	0	1	0	3	4	3	2	4	4	0
1	2	2	1	0	0	0	0	0	3	2	2	2	1
1	2	2	2	7	0	0	3	1	2	3	0	0	3
1	2	2	3	0	1	0	0	3	3	3	4	3	1
1	2	2	4	0	1	4	1	3	3	3	0	0	3
1	2	2	5	2	1	1	6	2	3	2	1	0	0
1	2	2	6	0	1	2	2	0	2	2	0	2	0
1	2	2	7	0	0	1	0	1	1	2	0	2	0
1	2	2	8	1	0	2	3	1	2	2	0	3	0

A	B	C	D	Growth (mm)									
2	1	1	1	7	14	8	11	10	8	11	11	8	13
2	1	1	2	11	12	9	9	11	6	3	12	14	6
2	1	1	3	0	18	4	5	7	11	8	19	13	9
2	1	1	4	9	5	3	5	4	8	19	12	4	17
2	1	1	5	5	6	16	18	5	6	7	7	7	2
2	1	1	6	21	2	9	2	8	17	9	8	4	13
2	1	1	7	2	11	18	4	36	7	0	13	14	11
2	1	1	8	10	4	5	0	0	11	0	3	2	0
2	1	2	1	6	7	11	6	8	8	8	9	2	8
2	1	2	2	15	10	15	9	19	0	10	15	3	6
2	1	2	3	2	1	9	3	0	0	2	1	1	1
2	1	2	4	7	4	2	8	6	4	2	10	3	7
2	1	2	5	6	0	0	1	17	6	9	7	3	10
2	1	2	6	11	11	10	4	16	9	2	10	7	3
2	1	2	7	0	12	11	1	0	6	2	0	10	0
2	1	2	8	0	3	0	4	0	6	1	9	14	5
2	2	1	1	7	6	6	5	16	10	7	7	9	9
2	2	1	2	21	8	4	12	10	7	10	36	13	5
2	2	1	3	4	16	26	10	11	11	23	11	11	9
2	2	1	4	12	12	19	28	22	0	6	8	11	27
2	2	1	5	0	7	7	2	4	3	4	0	9	6
2	2	1	6	9	9	1	7	14	7	9	3	6	7
2	2	1	7	12	4	10	0	6	10	10	11	8	18
2	2	1	8	7	9	8	6	10	5	0	8	9	1
2	2	2	1	0	8	4	7	6	9	8	5	7	8
2	2	2	2	9	13	20	7	6	9	4	13	8	0
2	2	2	3	4	9	9	5	5	10	5	6	10	1
2	2	2	4	7	7	8	7	16	18	13	19	9	17
2	2	2	5	0	7	3	3	4	6	9	4	14	4
2	2	2	6	2	5	6	7	1	9	9	7	5	1
2	2	2	7	1	12	9	9	21	11	10	33	9	8
2	2	2	8	12	7	1	0	10	7	20	11	0	

Appendix 4

Allele frequency table of 18 loci in 15 populations and three demes of Meesia triquetra. (EL = Ellesmere populations, YT = Yukon populations, AB = Alberta populations, D = Deme, and n = the number of individuals scored)

Isozyme	EL1	EL2	EL3	EL4	EL5	YT1	YT2	YT3	YT4
MDH-1									
(n)	30	29	0	30	30	30	30	29	30
A	0.00	0.00	----	0.00	0.00	0.17	0.90	0.21	0.00
B	1.00	1.00	----	1.00	1.00	0.83	1.00	0.79	1.00
MDH-2									
(n)	12	16	27	30	223	28	27	14	29
A	0.00	0.00	0.00	0.10	0.00	0.03	0.00	0.00	0.21
B	1.00	1.00	0.22	0.37	0.00	0.97	0.26	0.07	0.27
C	0.00	0.00	0.78	0.53	1.00	0.00	0.74	0.93	0.52
MDH-3									
(n)	30	29	29	30	30	27	23	30	28
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.83	0.89
B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.11
C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PGI-1									
(n)	27	0	29	30	30	29	29	30	30
A	1.00	-----	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Isozyme	EL1	EL2	EL3	EL4	EL5	YT1	YT2	YT3	YT4
PGI-2									
(n)	1	0	0	30	0	6	25	27	28
A	1.00	-----	-----	1.00	-----	0.17	1.00	1.00	1.00
B	0.00	-----	-----	0.00	-----	0.83	0.00	0.00	0.00
PGI-3									
(n)	29	30	30	25	30	30	30	30	9
A	1.00	0.93	1.00	1.00	0.00	0.17	0.00	0.20	0.00
B	0.00	0.07	0.00	0.00	1.00	0.83	1.00	0.80	0.89
C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11
PGM-1									
(n)	21	24	28	30	29	30	25	30	30
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
PGM-2									
(n)	30	30	30	29	30	30	30	30	30
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
PGM-3									
(n)	30	30	29	30	30	22	27	25	27
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Isozyme	EL1	EL2	EL3	EL4	EL5	YT1	YT2	YT3	YT4
TPI-1									
(n)	30	30	27	30	30	30	30	30	30
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
TPI-2									
(n)	30	30	27	30	30	29	30	30	30
A	0.00	0.00	0.00	0.00	0.00	0.90	0.00	0.00	0.93
B	1.00	1.00	1.00	1.00	1.00	0.10	1.00	1.00	0.07
GOT-1									
(n)	30	30	30	30	30	30	30	30	30
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
G3PDH-1									
(n)	20	27	0	26	0	0	0	0	0
A	1.00	1.00	----	1.00	----	----	----	----	----
G3PDH-2									
(n)	30	30	29	30	30	30	30	27	30
A	1.00	1.00	1.00	1.00	1.00	0.87	0.97	0.96	1.00
B	0.00	0.00	0.00	0.00	0.00	0.13	0.03	0.04	0.00
ALDO-1									
(n)	30	30	21	19	11	0	5	0	1
A	0.00	0.00	0.00	0.10	0.00	----	0.00	----	0.00
B	1.00	1.00	1.00	0.90	1.00	----	1.00	----	1.00

Isozyme	EL1	EL2	EL3	EL4	EL5	YT1	YT2	YT3	YT4
ALDO-2									
(n)	30	21	18	4	11	23	29	0	13
A	0.00	0.00	0.00	0.50	0.00	0.00	0.41	----	0.00
B	0.97	1.00	1.00	0.50	1.00	1.00	0.59	----	1.00
C	0.03	0.00	0.00	0.00	0.00	0.00	0.00	----	0.00
ADH-1									
(n)	0	0	0	23	0	0	4	2	0
A	----	----	----	0.40	----	----	0.25	0.00	----
B	----	----	----	0.60	----	----	0.75	1.00	----
ADH-2									
(n)	30	30	0	28	30	24	27	18	23
A	0.00	0.00	----	0.00	0.00	0.00	0.00	0.00	0.00
B	1.00	1.00	----	1.00	1.00	1.00	1.00	1.00	1.00

Isozyme	YT5	AB1	AB2	AB3	AB4	AB5	ELD	YTD	ABD
MDH-1									
(n)	30	30	15	30	30	30	30	30	30
A	0.10	0.60	0.07	0.43	0.10	0.27	0.00	0.00	0.30
B	0.90	0.40	0.93	0.57	0.90	0.73	1.00	1.00	0.70
MDH-2									
(n)	11	30	30	30	30	9	30	15	30
A	0.00	0.12	0.00	0.43	0.10	0.00	0.00	0.00	0.23
B	1.00	0.22	0.37	0.57	0.90	1.00	0.00	1.00	0.74
C	0.00	0.66	0.63	0.00	0.00	0.00	1.00	0.00	0.03
MDH-3									
(n)	26	30	30	30	30	30	30	30	30
A	1.00	0.96	1.00	0.93	1.00	1.00	1.00	1.00	0.00
B	0.00	0.04	0.00	0.07	0.00	0.00	0.00	0.00	0.97
C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
PGI-1									
(n)	30	30	29	29	30	0	30	30	30
A	1.00	1.00	1.00	1.00	1.00	----	1.00	1.00	1.00
PGI-2									
(n)	0	30	0	29	30	30	30	30	30
A	----	1.00	----	1.00	1.00	1.00	1.00	1.00	1.00
B	----	0.000	----	0.00	0.00	0.00	0.00	0.00	0.00

Isozyme	YT5	AB1	AB2	AB3	AB4	AB5	ELD	YTD	ABD
PGI-3									
(n)	30	30	30	30	30	30	30	30	30
A	0.17	0.00	0.17	0.00	0.27	0.00	0.00	0.00	0.10
B	0.83	1.00	0.83	0.93	0.73	1.00	1.00	1.00	0.90
C	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
PGM-1									
(n)	29	25	29	29	30	30	29	30	30
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
PGM-2									
(n)	30	30	30	30	30	30	30	30	30
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
PGM-3									
(n)	28	21	22	9	28	18	29	29	27
A	0.00	0.29	0.27	0.00	0.03	0.00	0.00	0.00	0.81
B	1.00	0.71	0.64	0.9	0.53	0.78	1.00	1.00	0.19
C	0.00	0.00	0.09	0.10	0.44	0.22	0.00	0.00	0.00
TPI-1									
(n)	0	30	30	29	30	0	30	30	26
A	----	0.00	0.27	0.00	0.23	----	0.00	0.00	0.77
B	----	1.00	0.73	1.00	0.77	----	1.00	1.00	0.23
TPI-2									
(n)	0	30	30	29	30	0	30	30	30
A	----	0.00	0.00	0.00	0.00	----	0.00	0.07	0.00
B	----	1.00	1.00	1.00	1.00	----	1.00	0.93	1.00

Isozyme	YT5	AB1	AB2	AB3	AB4	AB5	ELD	YTD	ABD
GOT-1									
(n)	0	30	0	0	30	0	30	30	30
A	----	1.00	0.00	----	1.00	----	1.00	1.00	1.00
G3PDH-1									
(n)	0	27	0	13	5	0	0	0	0
A	----	1.00	----	1.00	1.00	----	----	----	----
G3PDH-2									
(n)	30	30	25	17	30	30	30	30	30
A	0.97	0.93	1.00	0.88	1.00	0.87	1.00	1.00	1.00
B	0.03	0.07	0.00	0.12	0.00	0.13	0.00	0.00	0.00
ALDO-1									
(n)	0	4	27	5	0	0	30	0	26
A	----	0.25	0.00	0.00	----	----	0.00	----	0.11
B	----	0.75	1.00	1.00	----	----	1.00	----	0.89
ALDO-2									
(n)	0	26	27	13	29	0	30	0	26
A	----	0.08	0.00	0.08	0.41	----	0.00	----	0.00
B	----	0.92	1.00	0.92	0.59	----	1.00	----	1.00
C	----	0.00	0.00	0.00	0.00	----	0.00	----	0.00
ADH-1									
(n)	1	29	0	22	19	3	30	0	5
A	0.00	1.00	----	0.91	0.00	0.33	0.00	----	0.00
B	1.00	0.00	----	0.09	1.00	0.67	1.00	----	1.00

Isozyme	YT5	AB1	AB2	AB3	AB4	AB5	ELS	YTS	ABS
ADH-2									
(n)	24	29	0	22	18	13	30	26	19
A	0.00	0.00	----	0.09	0.27	0.61	0.00	0.00	0.95
B	1.00	1.00	----	0.91	0.73	0.39	1.00	1.00	0.05